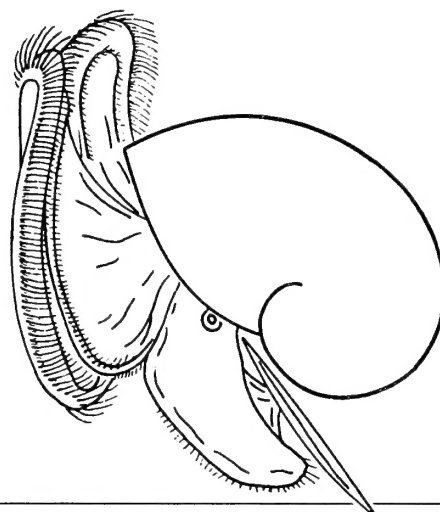


THE VELIGER

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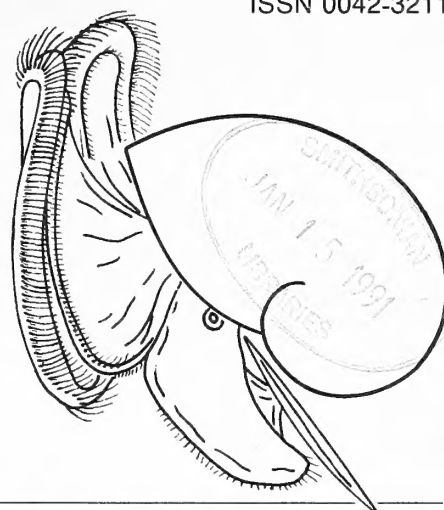
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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Early Life History of *Pleurobranchaea japonica* Thiele, 1925 (Opisthobranchia: Notaspidea)¹

by

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Abstract. The early life history of the notaspidean opisthobranch *Pleurobranchaea japonica* Thiele, 1925, was observed by light microscopy to elucidate the normal morphological changes in development from the egg to the crawling juvenile stage. This study confirmed that *P. japonica* has typical planktotrophic development (Thompson's development-type 1), and that the mantle originates from the mantle fold of the veliger larva. The larval shell is not cast off but is lost by dissolution or absorption. The origin and subsequent development of the mantle is the same as with another notaspidean, *Berthellina citrina* (Rüppell et Leuckart), though the developmental type of the latter species is lecithotrophic.

INTRODUCTION

Pleurobranchaea japonica Thiele, 1925, is the commonest notaspidean opisthobranch along the coasts of Honshû, Shikoku, and Kyûshû in Japan. *Pleurobranchaea japonica* lives on either muddy and sandy substrates in shallow water or on intertidal rocky shores. Many individuals are caught as a by-catch of commercial bottom trawling on muddy bottoms such as in Tokyo Bay, Middle Honshû. From February to June on the Pacific coast of middle Honshû, egg masses of this species are found on rocky substrates and seaweed in the intertidal zone or on shallow bottoms. As is the case with other members of the order Notaspidea, little is known about the life history of this species. The aim of the present study is to elucidate the normal embryological and post-embryological changes from the egg up to the juvenile stage, using light-microscopic observations on live animals reared in the laboratory. The only notaspidean whose development has been studied from the uncleaved egg to the juvenile is *Berthellina citrina* (Rüppell & Leuckart) (GOHAR & ABUL-ELA, 1957; USUKI, 1969).

MATERIALS AND METHODS

Most of the adult animals used for the present study were collected by a commercial trawler operating in the waters off Yokohama, Tokyo Bay, at depths of 20 to 40 m, during

the period from February to July 1987. Animals were also collected from the rocky shore of Nabeta Bay, Shimoda, in Izu Peninsula, Middle Honshû.

Adults were paired and reared in laboratory aquaria with running seawater.

Thirty-two egg masses that were laid by adults in captivity were kept in aquaria either with unstirred seawater that was changed daily, or they were placed under a tap of dripping seawater. Water temperature was not regulated, and ranged from $13.5 \pm 0.70^{\circ}\text{C}$ to $22.6 \pm 0.45^{\circ}\text{C}$. Just before hatching, all egg masses were placed in standing seawater overnight.

Newly hatched larvae were pipetted into beakers containing 2500 mL of seawater, which had been filtered through absorbent cotton. Cultures were stirred by a propeller at 60 rpm (Figure 1). Initial densities in each beaker were in the range of 125 to 750 larvae. They were fed daily on cultures of *Chaetoceros gracilis* Schutt, *Tetraselmis chui* Butcher, and *Nannochloropsis oculata* (Droop) Hibberd. The water temperature ranged from $22.2 \pm 0.85^{\circ}\text{C}$ to $24.7 \pm 0.55^{\circ}\text{C}$.

Juveniles that settled on the bottom of the rearing beakers were transferred into styrene plastic cylinders capped with netting that allowed overflow of excess seawater, which had been supplied through a tube. The range of temperatures during the rearing of juveniles was from $15.2 \pm 0.70^{\circ}\text{C}$ to $23.2 \pm 1.85^{\circ}\text{C}$. Juveniles were fed dried bonito powder or crushed cephalaspid (*Halos japonica* (Pilsbry)). They were also given microbiota grown on a polyvinyl plate that had been immersed in running seawater in an outdoor pool and washed with freshwater immediately

¹ Contribution No. 508 of the Shimoda Marine Research Center, University of Tsukuba.

² née Inoue.



Figure 1

A water circulating system with three 3000-mL beakers for rearing larvae of *Pleurobranchaea japonica*.

before being placed in the rearing cylinders. The development from egg to juvenile was observed under a light microscope using both anesthetized and non-anesthetized embryos, larvae and, juveniles. Anesthetization was made by the method of BICKELL & KEMPF (1983).

RESULTS

Oviposition

Paired adults repeated copulation and oviposition in the laboratory aquaria until death, with copulation and ovi-



Figure 2

Dorsal view of copulating animals, *Pleurobranchaea japonica*. Arrow indicates extended penis of the animal on the left.

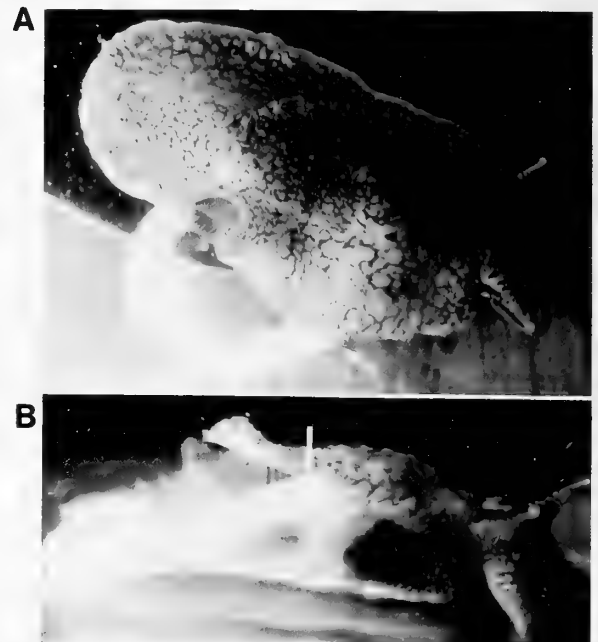


Figure 3

An animal in oviposition. A. Dorsal view with egg mass (arrow). B. Right lateral view of the same.

position usually occurring at night. Animals explore prospective mates with the papillose margin of the oral veil. Prior to copulation, two individuals orient in opposite directions with their right sides opposed. Each animal raises its right mantle edge, exposing its genitalia, and then extends the penis, which can swell to $\frac{1}{5}$ of the body length (Figure 2). The tip of the penis is used to feel for the vagina of the partner, which opens on the body wall at the base of the male genital organ.

Usually, both individuals lay egg masses on the same day or within two or three days after copulation (Figure 3). Oviposition tends to occur every four to six days in aquarium-held pairs. The maximum number of egg masses recorded for a single pair in captivity was 16, laid in 43 days, before the adults died.

Morphology of the Egg Mass

An egg mass consists of a cylindrical, gelatinous string, 8 to 10 mm in diameter and 19 to 64 cm (36.9 cm mean for 60 egg masses) in total length (Figure 4A). On average, each centimeter of gelatinous string contains 30 coils of spiral, membranous tube, holding 64 primary egg capsules per coil. Each primary egg capsule contains 1–12 (7.5 mean for 48 capsules from 12 egg masses) opaque primary oocytes (Figure 4B). Thus, a whole egg mass is calculated to contain about 530,000 primary oocytes. A thin gelatinous sheet, 2 to 3 mm in width, attaches the egg mass to the substrate in the form of a single or double anti-clock-

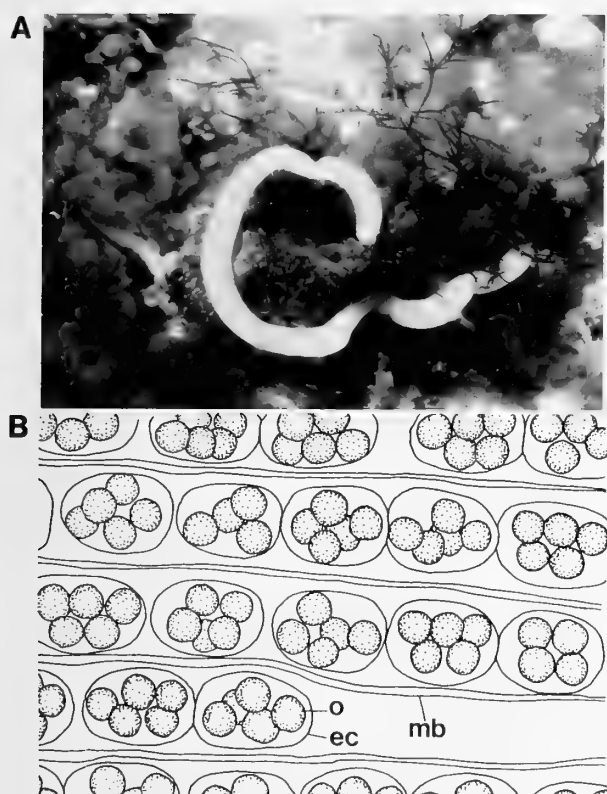


Figure 4

A. An egg mass on algae. Osezaki, Izu Peninsula, Middle Japan, 25 April 1989, water depth 6 m. B. Egg mass, magnified. Primary oocytes in the primary egg capsules are contained in a membranous tube. Key to the abbreviations used in Figures 4 to 14: a, anus; ah, adult heart; bm, buccal mass; e, eye; ec, primary egg capsule; ep, oesophagus; f, foot; g, gill; gc, green-colored cell; hb, hyaline rodlike bodies; i, intestine; j, jaw; ld, left digestive diverticulum; lh, larval heart; lm, larval mouth; m, muscle; mb, membranous tube; mc, mantle cavity; mf, mantle fold; mt, mantle; o, primary oocyte; ov, oral veil; p, propodium; pc, pigmented cell; po, postoral ciliary band; pr, preoral ciliary band; r, radula; rb, reddish body; rd, right digestive diverticulum; rh, rhinophore; rm, retractor muscle; s, shell; sc, statocyst; st, stomach; tb, transparent body; v, velum.

wise whorl 5 to 10 cm in diameter, sometimes with a trailing end.

Early Embryogenesis

Within an hour after oviposition, the fertilized primary oocyte releases two polar bodies, and the primary polar body divides into two.

The ovum, measuring 100 μm in diameter, undergoes spiral cleavage. A development schedule from oviposition to hatching is represented in Table 1. A ciliary band appears anterior to the blastopore. These cilia later lengthen and become the prototroch of the trochophore. Beating of

Table 1

Days from oviposition required for completion of each developmental stage at different water temperatures.

Stage	Days	Water temperature ($^{\circ}\text{C}$)
Blastula	1	18.0 ± 3.50
	2	14.4 ± 1.55
Gastrula	2	18.0 ± 3.50
	3	14.1 ± 1.00
Trochophore	4	14.8 ± 0.30
	5	14.5 ± 1.45
	6	13.7 ± 0.55
Hatching	6	21.0 ± 1.20
	7	15.4 ± 0.85
	8	14.0 ± 1.15

the prototroch cilia causes the trochophore to move actively in the egg capsule.

Larval Structure at Hatching

The newly hatched larva (Figure 5), has a sinistral shell that corresponds with THOMPSON's (1961) shell-type 1. The larval shell first appears at the posterior end of the trochophore, and it expands to cover all but the foot and velar rudiment as a single coiled larval shell of the veliger (Figure 6A). The larval shell is smooth, transparent, and colorless. On the inner lip region there are four to six ridges about 10 μm apart (Figure 6A–C). The outer lip is plain. The shell measures 152 μm to 183 μm (mean, 162.6 μm ; SD, 10.80; $n = 23$) in width at the time of hatching. This species possesses no operculum at any time during the entire developmental process.

In the trochophore stage, the region bearing the ciliary band protrudes to form an inverted heart-shaped velar rudiment in anterior view. The velar rudiment grows to be a velum typical of planktonic veliger larvae (Figure 5B, D, v).

The foot rudiment appears as a blunt process, which lengthens to be the slender, club-shaped larval foot about 80 μm in length. The ventral side of the foot bears short, crowded cilia and a blunt tip, which projects out from the shell aperture and has a tuft of long cilia measuring about 30 μm in length (Figure 5B, D, f).

In the newly hatched larva a fleshy ridge of the mantle fold extends along the inside of the aperture of the shell a little behind the shell margin (Figure 5B, D, mf). The ridge can be freely withdrawn and extended. The mantle cavity is limited to a narrow space between the mantle fold and the head (Figure 5B, mc).

The visceral region of the trochophore consists of three lobes of undifferentiated cells. These lobes differentiate to form the stomach and two digestive diverticula of the veliger (Figure 5B, D, st, ld, rd). A newly hatched larva has

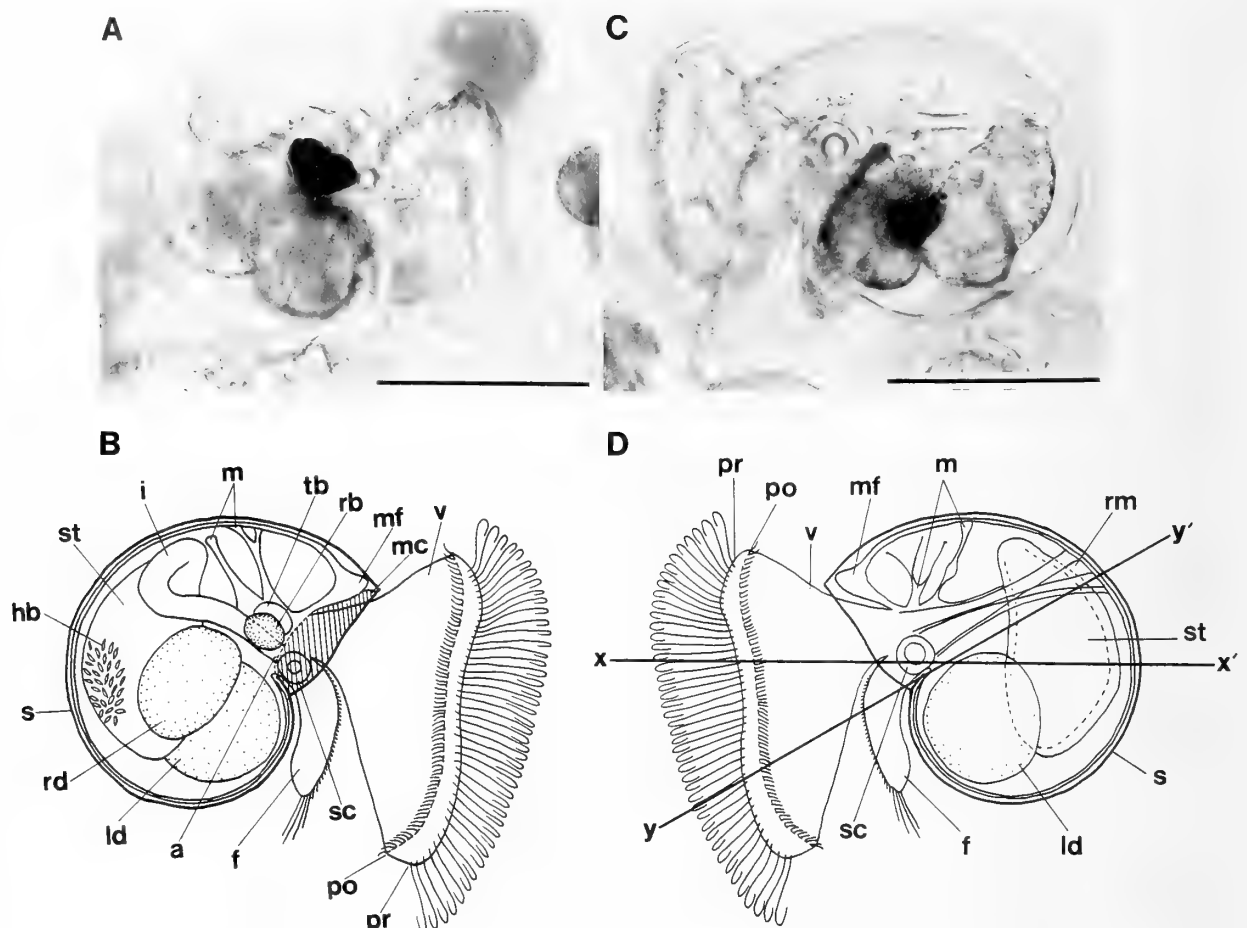


Figure 5

A. Right lateral view of veliger larva in egg capsule. Scale bar = 100 μ m. B. Diagrammatic representation of right lateral view of veliger larva. C. Left lateral view of veliger larva in egg capsule. Scale bar = 100 μ m. D. Diagrammatic representation of left lateral view of veliger larva. The two axes indicate the anterior-posterior axis (x-x') and ventral-dorsal axis (y-y') of the larval body, respectively. See Figure 4 for key to abbreviations.

a larval mouth between the preoral and postoral ciliary bands at the ventral base of the velar lobes. The larval mouth is surrounded by short, constantly beating cilia. A large left and the small right digestive diverticula occupy the ventral half of the visceral mass, and the difference in size between the two varies among individuals at hatching. An ellipsoidal stomach lies between the digestive diverticula and is connected with the oesophagus ventrally. Hyaline, rodlike bodies (THOMPSON, 1959) are distributed densely in the right posterior region of the stomach wall (Figure 5B, hb, and Figure 11). The stomach narrows dorsally into the intestine, which continues to the anal opening on the right side of the body in the mantle cavity (Figure 5B, i, a).

A globose structure appears on the right side of the body immediately after the formation of the prototroch, and gradually becomes distinct as it acquires a reddish color (Figure 5B, rb). Subsequently, a transparent structure,

which is similar in shape and size to the red one, appears beside and just above it (Figure 5B, tb).

A newly hatched veliger has velar and pedal retractor muscles (Figure 5D, rm). The bundles of retractor-muscle fibers originate at their attachment on the shell at the posterodorsal region just to the left of the midline, and extend past the left side of the stomach to insert into the head and base of the foot. Several small visceral muscles connect the visceral mass with the perivisceral epithelium (Figure 5D, m).

A pair of statocysts appears at the base of the foot rudiment on the ventral side of the body early in the morphogenesis from trochophore to veliger stages (Figure 5B, D, sc). Each statocyst contains a statolith, which constantly vibrates. Newly hatched veliger larvae lack eyes.

The behavior of newly hatched larvae was similar to that typical of planktotrophic opisthobranch veligers (HADFIELD & SWITZER-DUNLAP, 1984).

Morphogenesis from Newly Hatched Larva to Competent Larva

After hatching, larvae feed on phytoplankton and increase in size and morphological complexity as they approach the juvenile stage. Differences in initial larval density and rearing temperature affected survival rates and planktonic duration. The minimal period from hatching to metamorphosis was 15 days at an initial larval density of 250 individuals per 2500 mL ($22.8 \pm 1.7^\circ\text{C}$) and 17 days at 500 or 750 individuals per 2500 mL (both $23.7 \pm 0.85^\circ\text{C}$).

Shell width gradually increases up to $445.8 \mu\text{m}$ (mean; $n = 24$; SD, 40.14) just before metamorphosis (Figure 8). The general features of the shell exhibit no marked change from the time of hatching.

The velum becomes larger and more flexible as the larva grows. Each lobe can be extended up to 1 mm and cannot be withdrawn entirely into the shell cavity when the animal retracts. Several large green cells are scattered on the velar lobes (Figure 14B, gc). Larvae of *Pleurobranchaea japonica* feed in a manner typical of that for planktotrophic opisthobranch larva (THOMPSON, 1959).

The sole bears short cilia. The anterior edge of the foot widens and elevates to form a propodium (Figure 7D, p). The foot of a competent larva measures up to $300 \mu\text{m}$ in length, and has a thick propodium.

By 4 to 6 days ($22.7 \pm 1.6^\circ\text{C}$) after hatching, the mantle fold extends anteriorly and thickens to project beyond the shell aperture. Subsequent growth carries the mantle fold over the shell margin to the outer surface of the shell (Figure 9). As the larva grows, the reflected mantle fold bifurcates, leaving a narrow slit along the mid-dorsal line of the shell. At this time, the mantle fold can be withdrawn towards the shell aperture, but it can never be retracted into the shell cavity. Subsequently, the slit is gradually obliterated, starting from the anterior region of the mantle overgrowth. Just before settlement, the two lobes of the mantle fold completely fuse with each other at their posterior end to enclose the entire shell (Figure 7A, B). After fusion the mantle is never withdrawn to expose the shell. After 9 to 11 days ($23.1 \pm 1.95^\circ\text{C}$) from hatching, the dark brown pigmented cells, which are scattered among the mantle columnar epithelium, increase in number (Figure 9A, pc). The mantle cavity enlarges in the right lateroventral side of the body (Figure 7C, D, mc). A ciliated region appears in the middle of the mantle cavity just before settlement. The floor of the mantle cavity has a densely ciliated edge that slants to the right and is visible from the shell aperture.

A pair of jaws appears at the anterior extremity of the floor of the oesophagus. The appearance of the jaw is followed by the radula, which carries at least 12 lateral teeth in each of two rows (Figure 10). According to the present observations with a light microscope, the buccal mass including radula complex becomes evident in the larval buccal cavity just before metamorphosis. It is a cil-

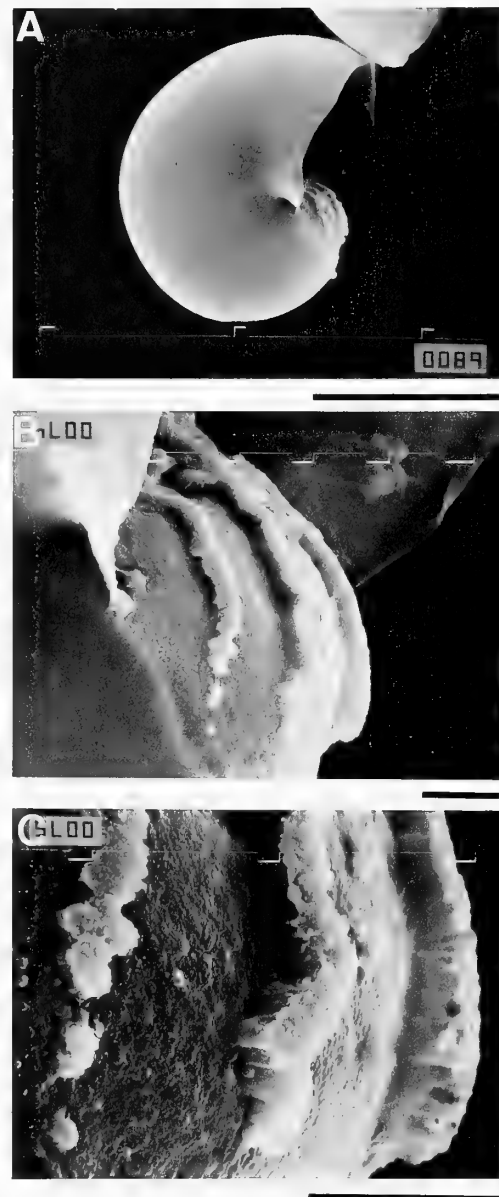


Figure 6

Larval shell. A. Shell of a newly hatched larva. Scale bar = $100 \mu\text{m}$. B and C. Ridges on inner lip, magnified. Scale bars = $10 \mu\text{m}$.

iated bulb with rather long and sparse cilia (Figure 13C, bm). The right digestive diverticulum decreases in size, becoming undetectable in live animals, while the left grows so as to occupy the ventral half of the visceral mass (Figure 7C, ld). Both digestive diverticula become dark brown during pelagic life. The stomach moves dorsally and slants anteriorly, as if displaced by the enlarged left digestive diverticulum (Figure 7C, st). The hyaline, rodlike bodies are as they were in the previous stage (Figure 11). The stomach lumen is divided into two parts with a constriction

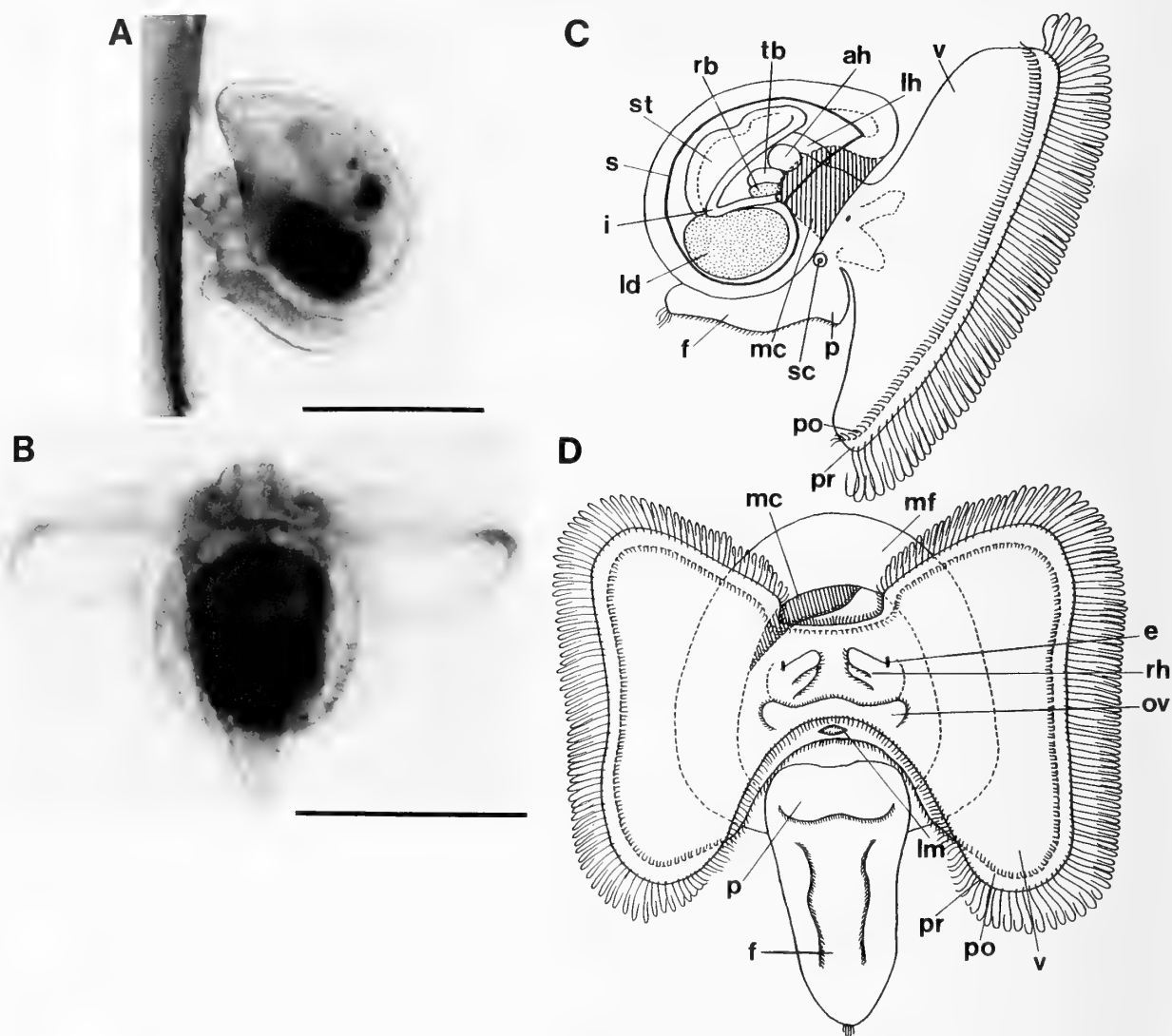


Figure 7

Full grown larva. A. Left lateral view of full grown larva. Scale bar = 500 μ m. B. Ventral view of full grown larva. Scale bar = 500 μ m. C. Diagrammatic representation of right lateral view of full grown larva. D. Diagrammatic representation of frontal view of full grown larva, foot extended. See Figure 4 for key to abbreviations.

at the middle. One stylelike food bolus is actively rotated in the stomach by the beating of cilia on the inner surface of the stomach wall. The intestine, which is roughly U-shaped, elongates gradually, and its turning point moves posteriorly (Figure 7C, i). The anus moves somewhat posteriorly on the right side of the animal as the mantle cavity continues to enlarge and deepen (Figure 7C, a).

The reddish globose structure above the anus gradually blackens and withers into a flat disc, while the transparent structure located next to the red one starts to swell (Figure 7C, rb, tb). These two presumptive excretory organs move somewhat posteriorly along with the anus.

The larval heart, a thin, membranous, regularly pulsing tube, develops 5 to 7 days after hatching ($23.2 \pm 1.95^\circ\text{C}$) (Figure 7C, 1h). It is located somewhat to the left of the animal's midline between the retractor muscle and the presumed excretory organs. The day after its appearance, the heart increases in size. This species possesses two hearts for a short period during the late larval life. In addition to the larval heart, the competent larva has a globose, transparent, membranous adult heart just above the presumed excretory organs (Figure 7C, ah). The two hearts do not synchronize, but pulse independently.

As the mantle fold encloses the shell, the internal organs

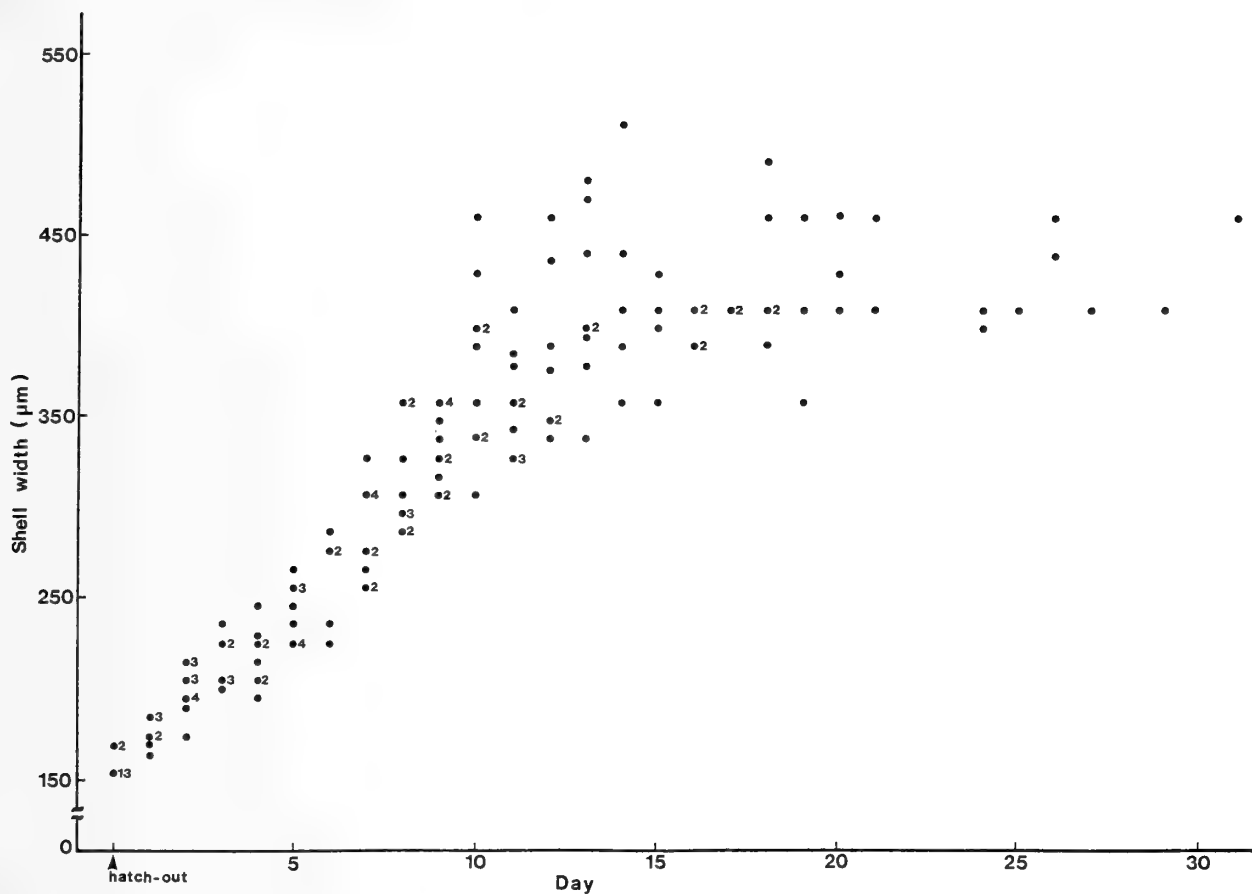


Figure 8

Growth of larval shell. Data points were obtained from different individuals reared in different beakers. The minimal period from hatching to metamorphosis was 15 days. Numerals attached to the points indicate the number of data points overlapping at that position.

become indistinct and the fate of the musculature cannot be traced in living animals.

After 5 to 7 days from hatching ($23.2 \pm 1.95^\circ\text{C}$), the eyes appear as small black spots located on the head just behind the velar base (Figure 7D, e). They become larger and more distinct within two or three days, but as the animal grows they become buried more deeply under the transparent head epithelium. The statocysts remain unchanged since their first appearance. The rudiments of the rhinophores and the oral veil appear before settlement (Figure 7D, rh, ov, and Figure 12). The oral veil first becomes visible at about the middle of the larval period as a small fleshy ridge situated somewhat below the center of the velum. This ridge has a row of short cilia and a pair of depressions at each end. The eyes underlie these depressions. The rhinophores first protrude from the depressions a few days after the appearance of the oral veil rudiment. Initially the oral veil grows anteriorly in the center, then along the margin of each side, forming three

ridges of which the central one thickens markedly. Finally, the oral veil gains volume, becoming trapezoidal in shape and covering the larval mouth. The rhinophores grow toward the center of the velum at first, and after, they change the direction of growth anteriorly and outwardly. In a competent larva, the rudiments of the oral veil and the rhinophores are miniatures of those in the adult.

Metamorphosis and Morphology of Juvenile

Through settlement and metamorphosis, the mode of larval life changes from pelagic to benthic, and the larva becomes a juvenile (Figure 13A–D). The loss of the velum signals this irreversible change of life.

The larval shell, which is entirely enclosed with the mantle fold, is never cast off, but gradually becomes smaller. This probably occurs by dissolution or absorption, and it starts from the inner lip of the shell immediately prior to the loss of the velum. The outline of the shell remnant

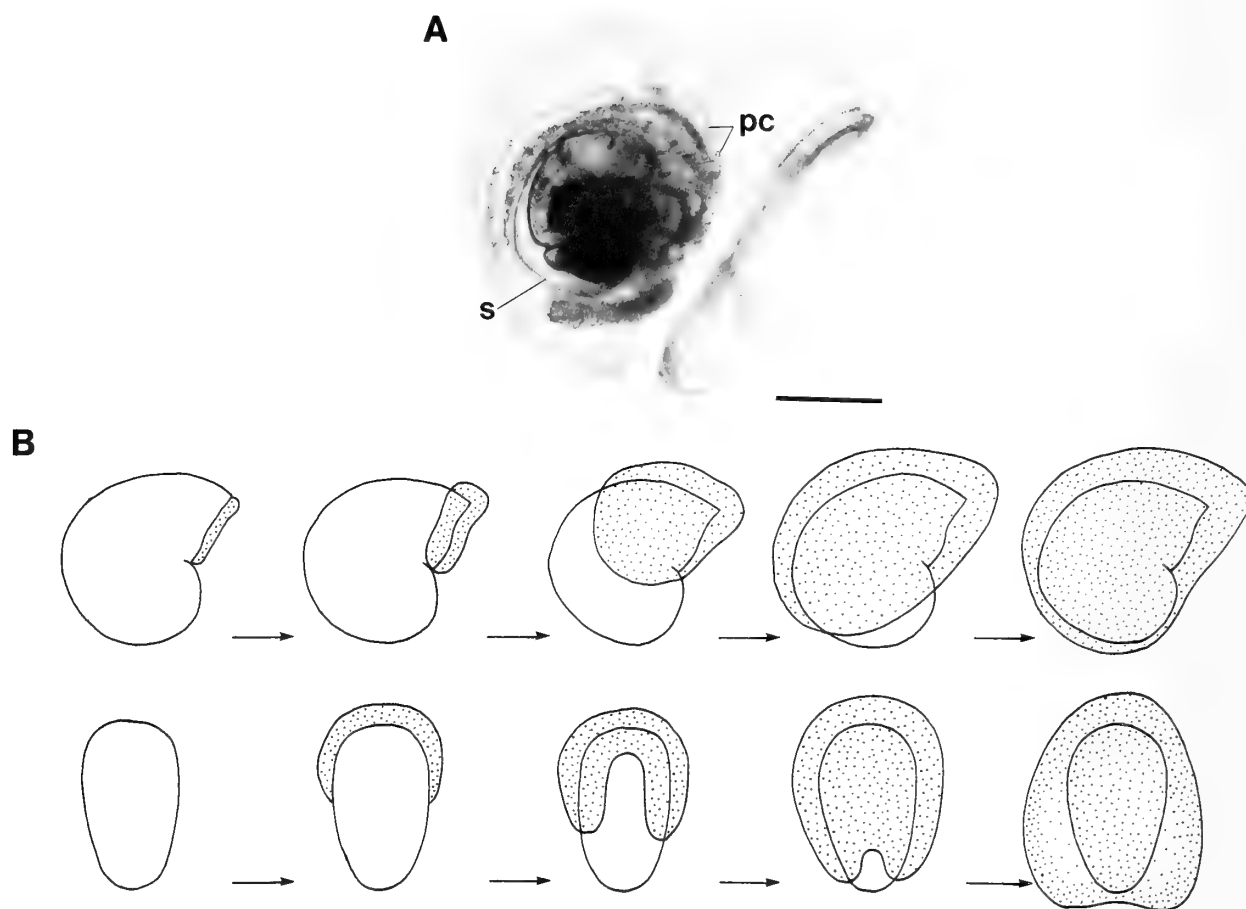


Figure 9

Growth of mantle fold. A. Right posterolateral view of a larva 20 days after hatching. The larval shell is exposed by the slit between the bilobed mantle fold. Scale bar = 200 μm . B. Diagrammatic representations of the growth of the mantle fold that finally covers the whole larval shell. Key: pc, pigmented cell; s, shell.



Figure 10

Radula and jaw plates of a full grown larva. Scale bar = 50 μm . Key: j, jaw; r, radula.

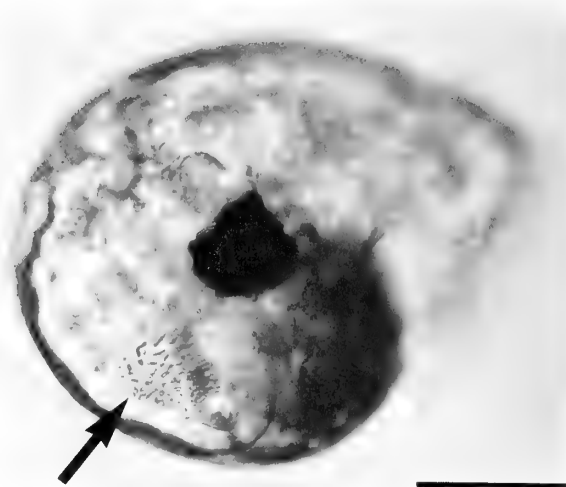


Figure 11

Hyaline rodlike bodies (arrow) in the right posterior region on the larval stomach wall. Scale bar = 50 μm .

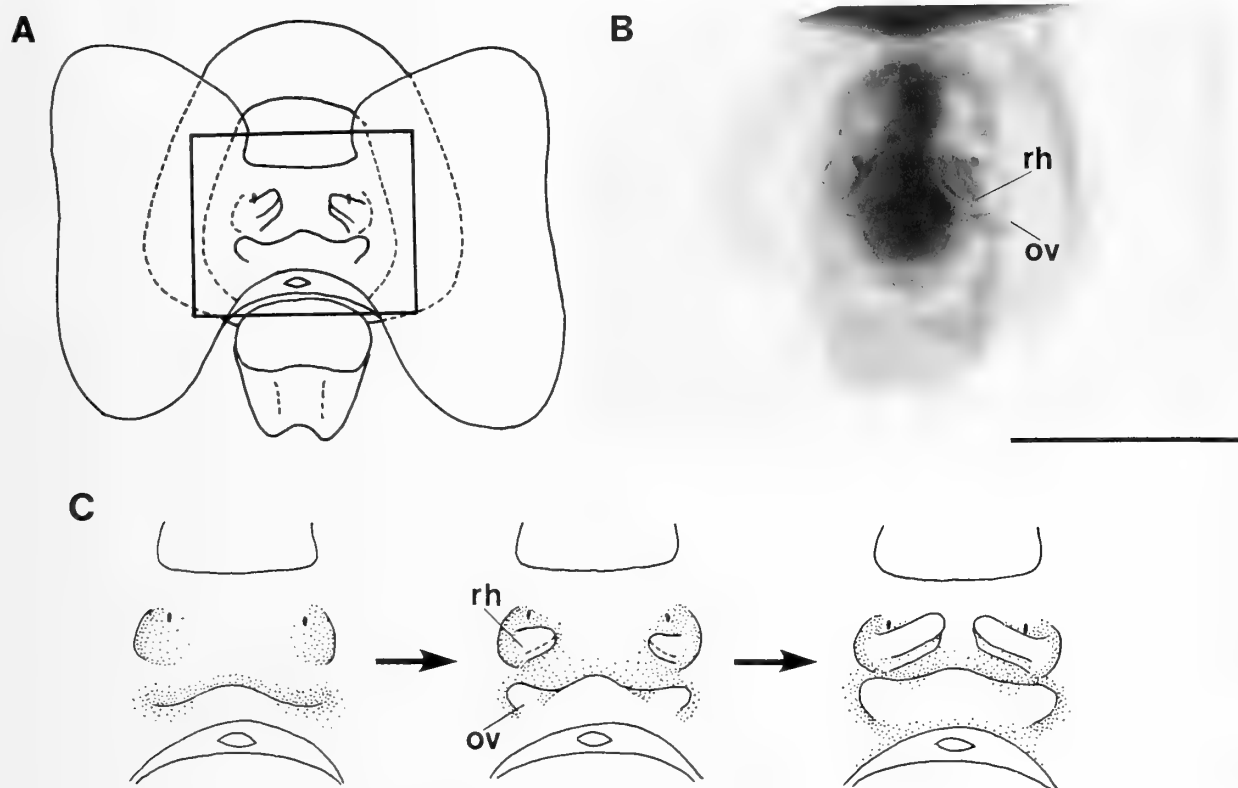


Figure 12

Growth patterns of rhinophores and oral veil. A and B. Frontal view of a full grown larva. Scale bar = 500 μm . C shows the growth series of the framed part in A. Key: ov, oral veil; rh, rhinophore.

is visible through the mantle as a reddish line (Figure 13B–D, s). Even after it has lost its velum, a juvenile still carries the remnant of the shell in the left posterodorsal region under the mantle (Figure 13C, D, s). Loss of the shell allows the visceral mass to settle within the foot, and the mantle cavity extends posteriorly along the right lateral side. As the shell remnant becomes reduced to an oval flat plate, the body of the juvenile also becomes flattened like that of the adult.

The ciliated cells of the preoral and postoral bands fall off and the other cells of the velum aggregate to create a pair of lobes with many large green cells on each side of the head (Figure 14A, B, arrow head, gc). These lobes gradually flatten and merge into the head epithelium. Some larvae lose one velar lobe a few hours ahead of the other. The time required from the loss of the ciliated cells to the completion of flattening of the lobes is usually half a day.

The morphology of the juvenile foot is not significantly different from that of the previous stage except for the loss of the tuft of cilia at the posterior tip of the foot. While the velum is being lost, the larva actively crawls about randomly on its well-developed sole. At the posterior region of the pedal sole of the juvenile there are one or two star-shaped spicules with a minute circle in the center. These

spicules are identical to those observed by GOHAR & ABUL-ELA (1957) in *Berthellina citrina*.

As the larval shell disappears, the juvenile extends its head anteriorly, flattening the body. The inner region of the mantle cavity is exposed externally as it moves to the right lateral side of the body. Subsequently, the border of the posterior end of the mantle fold fuses with the upper surface of the foot. The mantle, which is circular in shape at first with a diameter twice the width of the foot, becomes more slender and elliptical in shape. One to three pairs of dark reddish maculations appear near the margins of the mantle (Figure 15).

The juvenile begins feeding immediately after the loss of its velum. When feeding, the jaw plates and radula move anteriorly and posteriorly by the action of buccal musculature (Figure 13D, bm, j). The oesophagus elongates to the middle of the body and winds into an S-shape (Figure 13D, ep). The left digestive diverticulum occupies the posterior part of the animal (Figure 13C, D, 1d). The intestine could not be identified at this stage in this investigation because it was obscured by the thickened and pigmented mantle. The anus is situated laterally in the right mantle cavity, just posterior to the gill rudiment (Figure 13C, D, a, g).

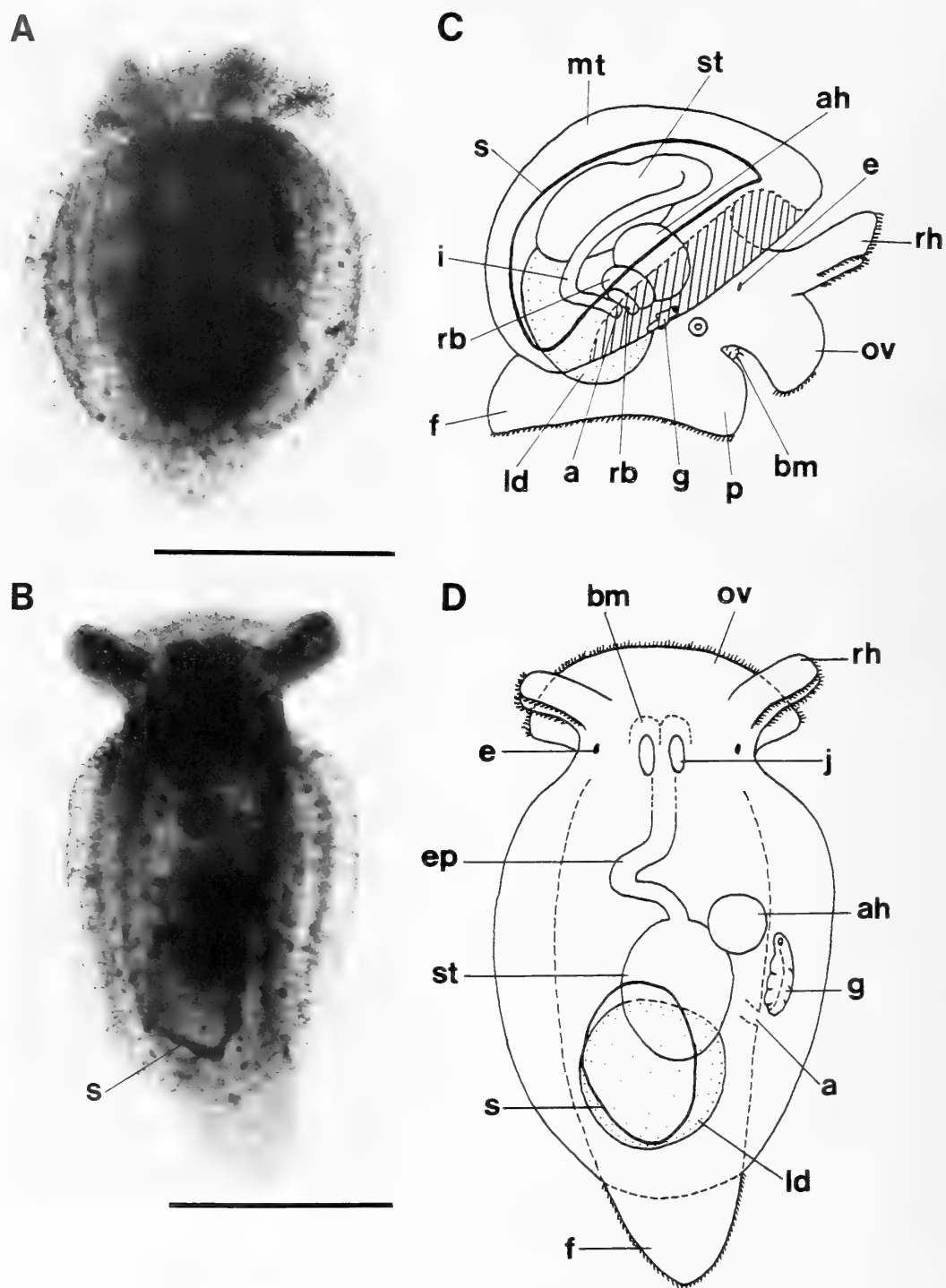


Figure 13

Juvenile of *Pleurobranchaea japonica*. A. Dorsal view of a juvenile immediately after loss of the velum. Scale bar = 500 μ m. B. Juvenile one week after loss of the velum, with a remnant of larval shell. Scale bar = 500 μ m. C. Diagrammatic representation of right lateral view of A. D. Diagrammatic representation of B. See Figure 4 for key to abbreviations.

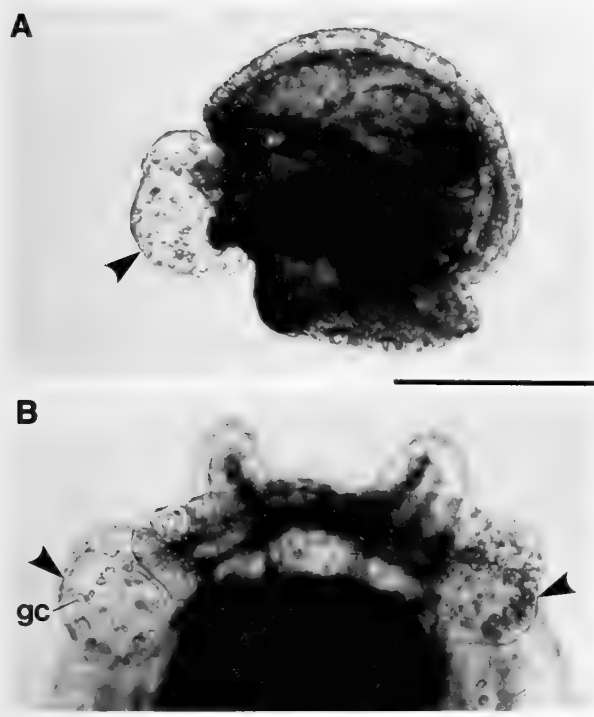


Figure 14

Larvae at settlement. A. Left lateral view of an animal with remnants of a disappearing velum (arrow head). Scale bar = 300 μm . B. Ventral view of the head region of an animal losing the velum (arrow head). Scale bar = 200 μm . Key: gc, green-colored cell.

The flat black disc just above the anus becomes smaller and disappears after settlement (Figure 13C, rb). The transparent globose structure seen earlier could not be observed when the animal had become flattened because of the thick overlying mantle.

After settlement the ciliary region in the middle of the mantle cavity develops into a ciliated gill rudiment (Figure 13C, D, gr). The length of the gill rachis and the number of alternating pinnae gradually increase; for example, two days after settlement an individual had only three pinnae on a rachis that was 132 μm long, whereas 15 days after settlement another individual had 10 pinnae on a rachis 305 μm long (Figure 16). The base of the rachis is tubular and located next to the adult heart (Figure 13C, D, g, ah). Just prior to settlement, the adult heart is larger than the larval one. Although the larval heart exists until settlement, it disappears immediately after.

The eyes gradually submerge under the head epithelium during the larval stages, although they are still visible for at least two months after settlement (Figure 13C, D, e). The statocysts exist on both sides of the pedal base under the anterior edge of the mantle of a juvenile. The oral veil, which reaches the basic adult shape prior to settlement, enlarges to become functional for feeding (Figure 13C, D,

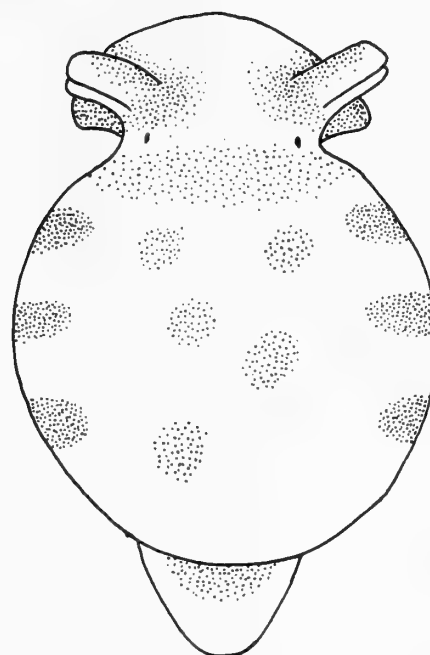


Figure 15

Dark reddish maculations on the body of a juvenile.

ov). A feeding juvenile senses the prey with the anterior edge of the oral veil, which is papillose and bordered with sparse tufts of short cilia. The dorsal surface of the oral veil, especially laterally, is dark red (Figure 15). The rhinophores are similar to those of the previous stage, except that dark red pigmentation appears near the bases (Figure 15). The cilia on the periphery of the rhinophores beat constantly.

Just before settlement, a larva creeps over the substrate with its velum extended. One that has lost its velum tends to crawl into a dark crevice. A juvenile will occasionally hang upside down from the water surface using surface tentation. The juvenile begins feeding on living or dead animal matter using its buccal mass immediately after metamorphosis. Juveniles are cannibalistic, and individuals displaying this tendency grow much larger than others.

Newly settled juveniles measure from 800 μm to more than 1000 μm in body length and from 500 to 900 μm in

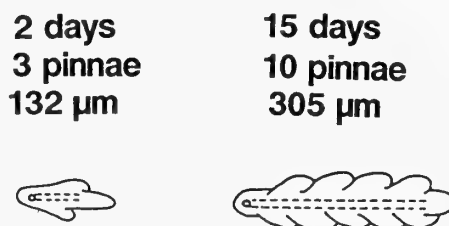


Figure 16

Growth of gill rudiment of a juvenile.



Figure 17

Juvenile. Dorsal view of a juvenile 2.5 months after loss of the velum. Scale bar = 5 mm.

body width. Juveniles survived at most two and a half months after settlement, and attained 12 mm in body length (Figure 17). The major cause of death was decreased water quality.

DISCUSSION

The newly hatched veliger larva of *Pleurobranchaea japonica* belongs to Thompson's development-type 1 (THOMPSON, 1967, 1976). Although planktotrophic, the larva of this species differs from others in lacking an operculum.

BONAR (1978) stated that when the nudibranch *Phestilla sibogae* lost its velum, all the ciliated cells selectively dissociated from the supporting tissue of the velum and were ingested as the first postlarval "meal." In *Pleurobranchaea japonica*, dissociation of the ciliated cells occurs as in *Phestilla sibogae*, but the ingestion of these cells by the settling animal was never observed. The remnants of the velum are incorporated into the head epithelium instead of forming a particular adult organ.

BONAR (1978) mentioned two origins for dorsal postlarval epidermis: one from the mantle fold and the other from the foot. In *Pleurobranchaea japonica*, the mantle fold is reflected over the apertural margin to enclose the shell completely prior to settlement. Thus, the dorsal postlarval epidermis is formed solely from the tissues of the mantle fold. The development of the mantle and the origin of the dorsal epidermis are the same as those hitherto reported for *Berthellina citrina* (GOHAR & ABUL-ELA, 1957; USUKI, 1969).

KRIEGSTEIN (1977), SWITZER-DUNLAP & HADFIELD (1977), PERRON & TURNER (1977), and BICKELL & KEMPF (1983) described post-hatching shell growth in the planktotrophic larvae of aplysiids and nudibranchs. In those

opisthobranchs the shell continues to grow until the mantle is retracted from the shell aperture. The post-hatching shell growth in *Pleurobranchaea japonica* is obvious. In this species, the mantle fold never attaches to the inner wall of the shell, but it can withdraw from the shell aperture. The mantle fold grows to reflect over the shell aperture instead of being retracted within the shell cavity. These features—mantle reflection that results in the complete enclosure of the larval shell, and shell growth that continues after mantle reflection—may be comparable with post-metamorphic growth of the mantle and shells in the cephalaspids *Philine aperta* and *Philine scabra* (HORIKOSHI, 1967). The fate of the larval shell in *Pleurobranchaea japonica* is hitherto unique among opisthobranchs lacking a shell in the adult stage.

THOMPSON (1959) stated that the right mid-gut diverticulum functions for yolk storage and plays no part in larval feeding. In *Pleurobranchaea japonica*, though the right digestive diverticulum decreases in size as the larva grows, its color darkens like that of the left one. This suggests that the right digestive diverticulum, like the left one, may function to a certain extent for larval feeding.

In *Pleurobranchaea japonica*, the oral veil and rhinophores are almost completely developed at settlement. We consider this to be an example of advanced differentiation of the cephalic structures among examples of opisthobranch development. In the lecithotrophic notaspidean *Berthellina citrina*, the rhinophoral rudiment differentiates prior to settlement, but completes differentiation much later in the juvenile stage (GOHAR & ABUL-ELA, 1957; USUKI, 1969). The formation of the oral veil in *P. japonica* is different from that in *B. citrina*; in *B. citrina* it is formed by the fusion of a pair of tentacles after settlement, whereas in *P. japonica* the oral veil rudiment is never divided into two tentacles. CHIA & KOSS (1982) suggest that rhinophores, complete with their ganglia, are essential for settlement and metamorphosis in the nudibranch *Rostanga pulchra*, whose metamorphosis is induced by the sponge prey of the adult stage. A prey-specific chemical stimulation of settlement and metamorphosis of *P. japonica* was not detected. Early formation of the rhinophores and the oral veil of *P. japonica* may enable the juveniles of this species to feed immediately after the loss of the velum. The rhinophores and oral veil of *P. californica* bear chemoreceptors that participate in food detection (BICKER *et al.*, 1982). Early formation of the oral veil and the early onset of feeding may be comparable with premetamorphic oral hood differentiation in the nudibranch *Melibe leonina* (BICKELL & KEMPF, 1983).

In agreement with THOMPSON (1958, 1976), no organ was found to exhibit torsion as a mechanical process during the embryogenesis and larval development of *Pleurobranchaea japonica* in the present observation. As the shell dissolves in the later larval stages, the mantle cavity deepens and changes the direction of the opening, accompanied by the posterior displacement of the anus. This change may be regarded as detorsion in this species, as HYMAN

(1967) regarded it on the basis of many works by previous authors. This displacement, however, is not accompanied by a rotation of whole visceral organs, but only by a deepening of the mantle cavity, accompanied by elongation of alimentary canal and anal displacement.

Pleurobranchaea japonica seems to require no external stimulus for settlement and metamorphosis. This may reflect the fact that the adults have no specific prey, but eat a broad spectrum of food.

This study clarified the general events during the early life history of *Pleurobranchaea japonica*, which have not hitherto been documented. Such contributions are needed to clarify the infra- and intra-order relationships of the Notaspidea. Such details as cleavage, neural development, and others remain to be studied; these gaps will be filled by future study.

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Recruitment in the Deep-Sea Wood-Boring Bivalve *Xylophaga atlantica* Richards

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Abstract. Recruitment in a deep-sea wood-boring bivalve, *Xylophaga atlantica* Richards, 1942, was monitored over a two-year period from July 1987 to June 1989 at two locations on the edge of the continental shelf south of Cape Cod in the western North Atlantic Ocean. Average recruitment densities of *X. atlantica* in test panels varied from 0 to 30 animals/cm². At the 100-m site, peak settlement was observed between September and December 1987 with a smaller peak from June to September 1988. Recruitment rates at this site declined sharply between January and May in 1988 and 1989. The recruitment rate at the 200-m site remained at relatively high levels during the months of February through April with a significantly higher peak during 1989 as compared to 1988. Low recruitment was observed from May through December in 1987 and 1988. Significant differences in recruitment between the two sites were observed for all sampling periods except for the period April through June, when recruitment was low at both sites.

INTRODUCTION

Settlement and metamorphosis of most deep-sea sessile marine invertebrates are poorly understood. The pholad subfamily Xylophagainae, whose members have adapted to utilizing wood in the deep sea, has many species distributed throughout the world's oceans (KNUDSEN, 1961). Although the distribution of individual species in this subfamily is thought to be temperature dependent (PERKINS, 1974), Xylophagainae distribution is also determined by the presence of wood on the sea floor (TURNER, 1973). Wood reaching the deep sea is rapidly decomposed, principally through the activity of these bivalves, which convert the woody plant material into a food source for detritus feeders, predators, and filter feeders (TURNER, 1977).

Xylophagainae presumably utilize wood for both food and shelter, as do shallow-water teredinids, although *Xylophaga* has been found embedded in the gutta-percha sheaths of submarine telegraph cables (PURCHON, 1941). There is some controversy over how wood is broken down and utilized by these organisms. Cellulase activity of symbiotic bacteria located in the gland of *Deshayes* is thought to be the mechanism in some teredinid species (WATERBURY *et al.*, 1983). Cellulase activity has been confirmed for *Xylophaga dorsalis* (PURCHON, 1941) although the source of this activity has not been determined.

Since the advent of the New England offshore lobster fishing industry in the 1960s, *Xylophaga atlantica* has contributed significantly to the deterioration of the wooden

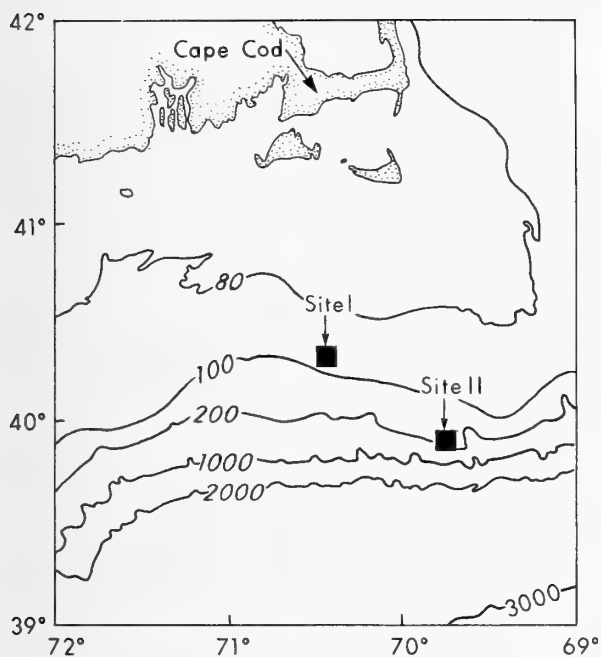


Figure 1

Sampling Sites I and II off southeastern New England, USA. Depth contours in meters.

lobster traps. Untreated traps are destroyed in less than one year, creating economic concerns for the fishermen (Dow, 1950). Although vinyl-covered wire-mesh traps are available, wood traps are preferred because of their low initial cost, reparability, perceived higher catch rates, and potentially longer length of service (DEALTERIS *et al.*, 1988).

BERG *et al.* (1987) recently reported temporal variability in the recruitment of several invertebrate species on Georges Bank, including the bivalve *Xylophaga atlantica*. The range of *X. atlantica* extends from the St. Lawrence estuary, at 48°N, south to Cape Henry, Virginia, at 36°N, in depths from 5 to 3000 m (TURNER, 1971). Other wood-boring pholads sympatric with *X. atlantica* include *Xylophalas altenae* Turner, 1972 and *Xylophaga* species 1, 2, 3, and 4 (BERG *et al.*, 1987). Relative geographic and seasonal distribution and recruitment patterns are unknown for *Xylophaga atlantica*. The present study examined the seasonal recruitment of *Xylophaga atlantica* in the western North Atlantic at two New England sites. The objective of this study was to provide information on recruitment patterns of *Xylophaga atlantica* and to provide information to the fishermen on probable times of heaviest infestation of offshore wooden lobster traps.

MATERIALS AND METHODS

The *Xylophaga* samples were collected at two sites at the edge of the continental shelf south of Cape Cod (Figure 1). Site I was located at the 100-m contour (40°26'N,

70°28'W). Site II was situated at the 200-m depth contour (39°55'N, 69°44'W).

Vinyl-coated wire-mesh racks, each containing 24 wood panels, were placed inside vinyl-coated wire lobster traps, which were fished in a trawl formation by participating offshore lobster fishermen (Figure 2). A trawl consisted of many traps tied at 30-m intervals along a single bottom line buoyed at each end. Two racks in each of two trawls (not more than 20 km apart) were deployed at each site.

Each rack held 12 rough oak panels on one side and 12 rough-smooth pine panels on the other. Each panel was retained in a compartment in the rack with 1.0 cm clearance between panels for water to circulate. The panels were cut to a uniform size of 20 cm high × 8 cm wide × 2.5 cm thick. Only oak panels 2, 3, 4, 5, and 6 were used to estimate recruitment densities (Figure 2). Pine panels were used in a concomitant field study of small-scale larval settlement patterns (ROMEY, 1989).

The racks were collected at intervals ranging from 29 to 212 days and the exact depth and location were recorded. The racks were stored in a circulating seawater tank on the vessel until their return to the docks several days later. The racks were then maintained in chilled seawater tanks while toxicological studies (DEALTERIS *et al.*, 1988) were performed. After completion of these experiments, panels were preserved by desiccation.

Recruitment is an observer-defined unit where the organism attains a predefined size or age (KEOUGH & DOWNES, 1982). Recruitment and settlement are not identical owing to a number of factors such as postlarval mortality (BUTMAN, 1987). In this paper, a recruited *Xylophaga atlantica* is one that has settled, undergone metamorphosis, and burrowed into the wood to form a visible bore hole. Subsequent mortality was not determined. Slight pits or depressions were counted only when animals were present. Losses from the manipulation of the panels were assumed to be the same for all samples.

The density of specimens recruited per panel was obtained by counting the number of bore holes/cm². The samples were taken using a diagonal transect method to survey all parts of the panel face equally. A measured cm² grid was laid over the panel face and 32 one-cm² areas/face were examined (Figure 3). The sides of the panel were not counted owing to differential settlement patterns, as indicated by preliminary results from ROMEY (1989). Whole animals were later removed, identified, and measured for a concomitant growth study (ROMEY, 1989).

A recruitment rate index was then calculated in order to compare recruitment between panels and racks that had collected larvae for differing periods of time. This index (RI) is a rate function:

$$RI = (AVG/T) \times 100$$

where AVG is the average number of recruits/cm² for the rack and T is the time in days that the panel was on the sea floor. Panels within a rack were considered to be re-

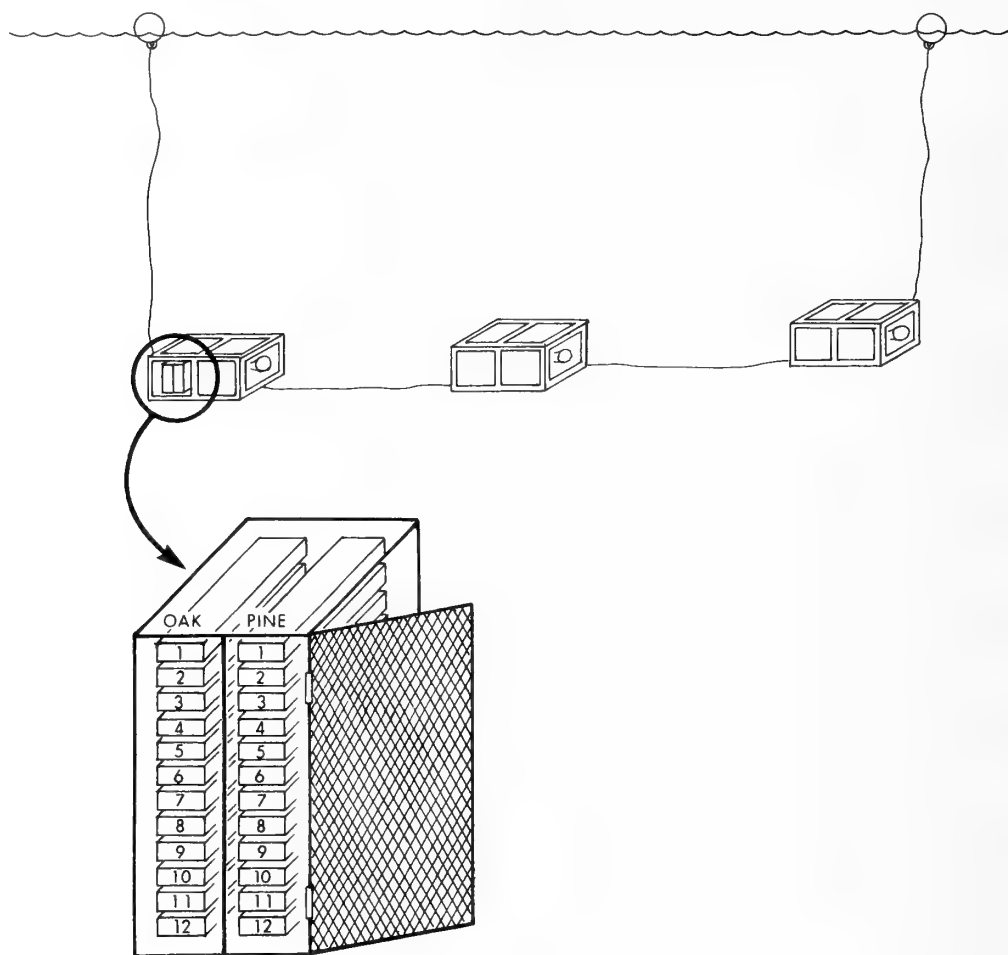


Figure 2

Vinyl-coated wire racks, each containing 24 wood panels, were placed inside vinyl-coated wire lobster traps, which were fished in a trawl formation.

peated measures and variation between and within trawls in a site was found to be statistically insignificant (ANOVA, $P > 0.10$; ROMÉY, 1989). An average recruitment for the racks was calculated using panels 2, 3, 4, 5, and 6. The outside panel was not used in the average because it exhibited a significantly higher recruitment (ROMÉY, 1989).

RESULTS

Xylophaga atlantica was the principal species encountered during this investigation. In Site II, an undescribed species of *Xylophaga* was occasionally found on the panels. No teredinid species were encountered. Identification of the specimens was provided by R. D. Turner. Voucher specimens have been deposited in the Museum of Comparative Zoology at Harvard University.

Recruitment at Sites I and II ranged from an average of 0 to 30 animals/cm² depending on season and location.

At Site I, 16 racks were collected over the two-year investigation period (Table 1). Moderate recruitment ($RI < 3$) was observed between August and October 1987; low recruitment was observed from January 1987 to May 1988, and from September 1988 to July 1989. A peak in recruitment ($RI > 9$) occurred between September to December 1987, with a smaller peak ($RI = 4$) from June to September 1988 (Figure 4a).

Sixteen racks were retrieved at Site II. Data were not available from October 1987 to February 1988 owing to the loss of the sampling panels. Low recruitment ($RI < 3$) was observed in samples collected from September 1987 through January 1989. High recruitment occurred from January to May 1989 ($RI = 19$) with a maximum recruitment occurring from March through April 1989 ($RI = 36$) (Figure 4b).

Recruitment patterns differed between the two sites. Significant differences (paired t -test, $P = 0.25$; SOKAL &

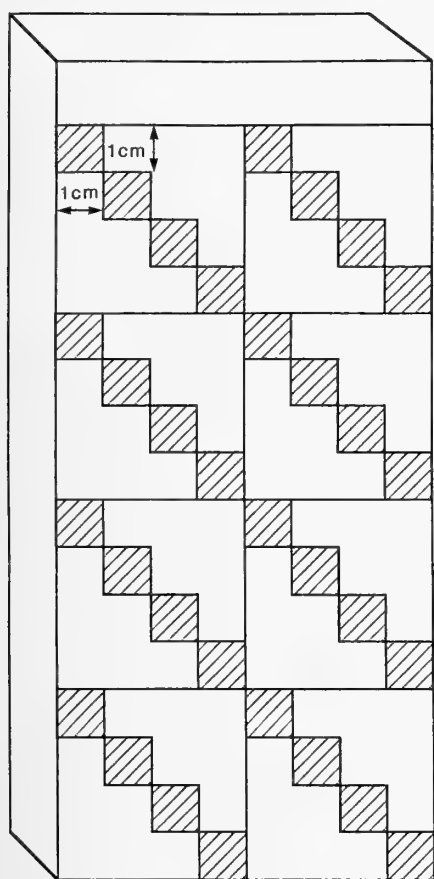


Figure 3

A measured cm^2 was laid over the panel face and 32 one- cm^2 areas were examined in a cross grid pattern.

ROHLF, 1981) were observed for all sampling periods except for April to June 1988, when recruitment was low for both sites. The highest recruitment ($\text{RI} = 36$) occurred at Site II, whereas the highest recruitment measured at Site I reached only $\text{RI} = 15$.

DISCUSSION

The seasonal and geographical distribution of an organism is affected by two factors: its immediate environment and the particular life history that the organism has developed to live in the overall environment (WILLIAMS, 1975). *Xylophaga* is the first reported group of opportunistic organisms from the deep sea (TURNER, 1973). This group is characterized by high population densities, high fecundity, early maturity, rapid growth, delayed metamorphosis, and protandrous hermaphroditism (TURNER, 1973).

Wood carried out to sea and sinking at variable rates and locations produces a patchy environment on the sea floor. However, the occurrence of wood at the bottom of the sea must be a predictable event (DAYTON & HESSLER,

1972) which allowed for the evolution of this entire subfamily of woodborers (TURNER, 1973). Sources of wood are many (including wood carried by rivers, canoes, boats, and lobster traps). Wood is probably not distributed randomly, but rather follows broad patterns based on currents and sources of wood. Most likely, the direction and magnitude of the currents regulate both the distributions of wood and pholad larvae. Near-bottom currents may play a role in small-scale recruitment patterns. The relationship between boundary layer flow and recruitment of barnacle cyprids was found to be highly significant (CRISP, 1955). Differential post-settlement mortality might also be a factor in the observed recruitment patterns (BUTMAN, 1987).

Measurement of the currents from nearby sites (HOUGHTON *et al.*, 1988) was used to calculate the potential range of a passively drifting larva of *Xylophaga atlantica*. The average benthic current of 2.5 cm/sec could theoretically move these organisms more than 2 km/day or up to 70 km/month in a southeasterly direction. CULLINEY & TURNER (1976) kept larvae alive in the laboratory for two months without the larvae undergoing metamorphosis. During this time, they would have been capable of traveling more than 140 km with the currents. If the larvae were able to migrate vertically, they would be able to select currents that transport them into areas with suitable substrate and perhaps even return them to the general location where spawning had occurred. Slow development and delayed metamorphosis at colder temperatures might also enhance dispersal capabilities of the larvae (PECHENIK, 1980).

Although the actual settlement of *Xylophaga atlantica* has never been observed in the laboratory, development of the larvae from the fertilized egg to the pediveliger (settlement stage) has been reported. CULLINEY & TURNER (1976) reported that *X. atlantica* releases eggs when the temperature rises from 4°C to 9°C . BERG *et al.* (1987) reported gonadal ripening of *Xylophaga* in late summer when the temperature exceeds 10°C . CULLINEY & TURNER (1976) predicted a long larval planktonic stage, and suggested that the larvae probably would not settle and undergo metamorphosis until the fall or winter.

Although data on temperature are not available for the two study sites, it has been suggested that seasonal variations do occur on the bottom. HOUGHTON *et al.* (1988) reported a peak of 14°C in late November and a low of 5°C in February in a site located south of Cape Cod on the shelf-slope interface at a depth of 75 m. A three-year time series of temperatures on Georges Banks collected by BERG *et al.* (1987) also supports these observations. Station Q from BERG *et al.* (1987) coincides with our present Site I. If seasonal tendencies are assumed to be similar year to year, these temperatures can be compared to those affecting *Xylophaga* recruitment at Site I. A steady rise in mean bottom temperature occurred from February through October, reaching a peak of 15°C in November. The temperature rose above 10°C from August through October, corresponding to peak recruitment at Site I during 1987.

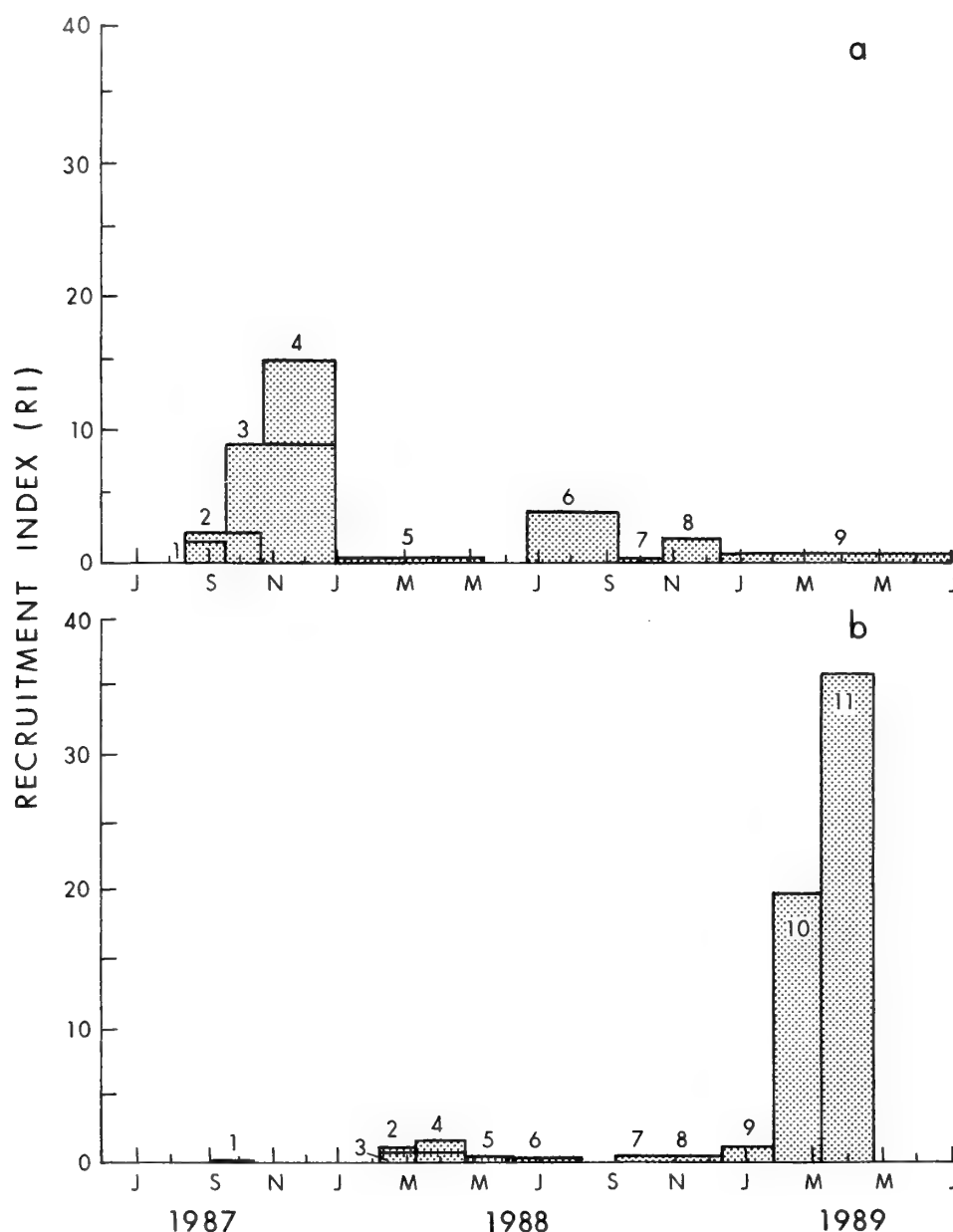


Figure 4

Recruitment indices (RI) at Sites I (a) and II (b). Data are plotted over the period of panel submergence. Recruitment index is the average number of recruits/cm² divided by the number of days on the sea floor, multiplied by 100 (see text).

A smaller peak was observed from July to September 1988. Slight yearly temperature variations might account for these shifts in peak recruitment.

At depths of approximately 200 m at the edge of the continental shelf, the temperature ranges from 10 to 12°C throughout the year (BEARDSLEY *et al.*, 1985; HOUGHTON *et al.*, 1988). Temperature would not be a good physical

trigger to initiate spawning in these areas because it does not have a regular annual variance. Other environmental cues affecting the benthos could be chemical or light that might penetrate to some extent. Plankton are believed to supplement the nutritional requirements of teredinids (PECHENIK *et al.*, 1979) and some species can grow and reproduce only when their wood diet is supplemented with

Table 1

Summary of the data obtained from the two collection sites. (Duration = number of days panels were subjected to recruitment at sea floor; AVG = average number of recruits per 4 cm² ($n = 80$); SE = standard error of the mean ($n = 80$); RI = recruitment rate index, which equals (avg/4)/days \times 100.

Site	Dates	Duration (days)	Rack	Avg	SE	RI
I	12 Aug. 87–22 Sep. 87	40	8a	1.97	0.27	1.23
		40	2a	2.34	0.23	1.46
	12 Aug. 87–19 Oct. 87	68	3a	5.25	0.44	1.93
		68	7a	5.85	0.39	2.15
	22 Sep. 87–22 Dec. 87	92	8b	29.37	1.32	7.98
		92	2b	36.67	1.87	9.96
	19 Oct. 87–22 Dec. 87	64	3b	32.24	2.16	12.59
		64	7b	57.03	2.86	22.28
	22 Dec. 87–13 May 88	143	8c	1.85	0.24	0.32
		143	2c	2.04	0.25	0.35
		143	3c	1.45	0.19	0.25
		143	7c	4.54	0.50	0.79
	19 Jun. 88–8 Sep. 88	51	8e	8.03	0.54	3.94
	8 Sep. 88–18 Oct. 88	41	2f	0.36	0.01	0.22
	18 Oct. 88–7 Dec. 88	51	8g	3.35	0.43	1.64
	7 Dec. 88–6 Jul. 89	212	2h	3.35	0.39	0.39
II	10 Sep. 87–15 Oct. 87	35	4a	0	0	0
		35	5a	0	0	0
	10 Feb. 88–10 Mar. 88	29	4b	2.35	0.26	2.03
		29	5b	2.35	0.26	2.03
	10 Feb. 88–24 Apr. 88	75	1a	4.86	0.41	1.62
		75	6a	8.81	0.57	2.94
	10 Mar. 88–24 Apr. 88	45	4c	2.87	0.28	1.60
		45	5c	6.73	0.43	3.74
	24 Apr. 88–7 Jun. 88	44	4d	0.78	0.12	0.44
		44	5d	2.18	0.28	1.24
	7 Jun. 88–4 Aug. 88	58	4e	0.25	0.01	0.11
	11 Sep. 88–13 Oct. 88	31	4h	0.48	0.01	0.38
	13 Oct. 88–7 Dec. 88	56	4i	1.65	0.18	0.74
	7 Dec. 88–20 Jan. 89	45	4j	3.07	0.29	1.71
	20 Jan. 89–11 Mar. 89	51	4k	38.32	2.28	18.78
	11 Mar. 89–24 Apr. 89	45	5l	64.70	2.34	35.94

phytoplankton (KARANDE *et al.*, 1968). Plankton may play a role in *Xylophaga* nutrition, growth, and spawning, that is currently undiscovered.

ACKNOWLEDGMENTS

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for this study. Deepest sympathies are extended to the families of the captain and crew.

This is contribution number 2536 of the University of Rhode Island, College of Resource Development, Agricultural Experiment Station, Kingston, Rhode Island 02881, USA.

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Functional Anatomy of *Castalia undosa undosa* (Martens, 1827) (Bivalvia: Hyriidae)

by

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Abstract. *Castalia undosa undosa*, Martens, 1827, is a member of the family Hyriidae, the distribution of which is restricted to South America. In Brazil the species occurs in the center-south region, corresponding to the upper Paraná River. These medium-sized mollusks live buried in muddy substrata, are slightly heteromyarian, and are dioecious, with sexual dimorphism evident in the shell conformation. The siphons are simple (type AII of Yonge, 1957), and mantle fusion occurs only through the inner fold. The incumbent siphon has tentacles originating from the inner fold and the excurrent siphon exhibits a few tubercles, probably of sensory function. The ctenidia are of type D (of Atkins, 1937). Internally, females possess a well-developed marsupium in the inner demibranch in which eggs are incubated. The stomach is a type IV structure (of Purchon, 1958), and is quite uniform when compared to that encountered in other freshwater bivalve families.

INTRODUCTION

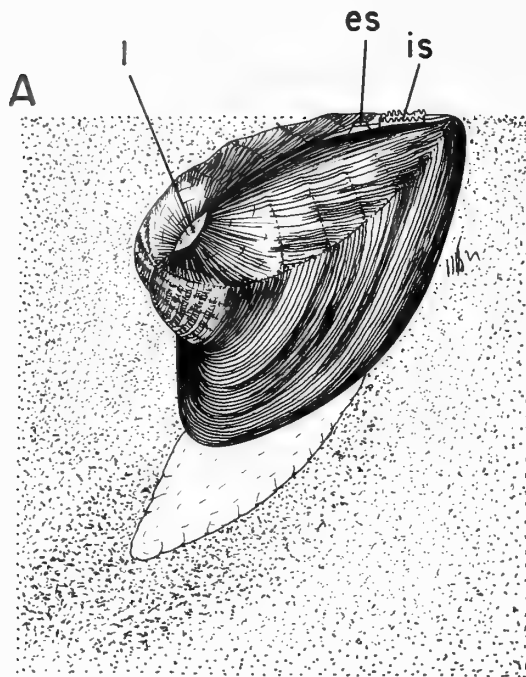
The South American family Hyriidae Fleming, 1828, is represented by a single subfamily, Hyriinae Swainson, 1840, with two tribes, Castaliini and Diplodontini, both of Parodiz & Bonetto, 1963. Of the five genera belonging to the tribe Castaliini which, according to BONETTO (1965), is widely distributed throughout the South American continent and particularly in Brazil, only three were detected by LANGE DE MORRETES (1949)—i.e., *Castalia*, *Castalina*, and *Callonaia*—whereas *Chevronais* and *Castaliella* were not mentioned. In a review of the tribe Castaliini, BONETTO (1965) discussed the value of the different genera and concluded that only *Castalia* and *Callonaia* should be considered, admitting the introduction of subgeneric categories only in the genus *Castalia*. Thus, according to BONETTO (1965), *Castalia undosa* Martens, 1885, has two subspecies; *C. ambigua* Lamarck, 1819, has four subspecies; and *C. psammoica* Orbigny, 1835, and *C. sulcata* Krauss, 1849 have three subspecies each; *Callonaia* has only the species *C. duprei* Recluz, 1843. Among the papers available on the anatomy of South American Unionacea, particularly outstanding are those by MANSUR (1972, 1973), HEBLING & PENTEADO (1974), HEBLING (1976), and MANSUR & ANFLOR (1981). Other investigators, in studies on the genus *Castalia*, have referred only to branchial openings,

ctenidia, palps, and muscles (IHERING, 1891, 1893; ORTMANN, 1921; BONETTO, 1961, 1965).

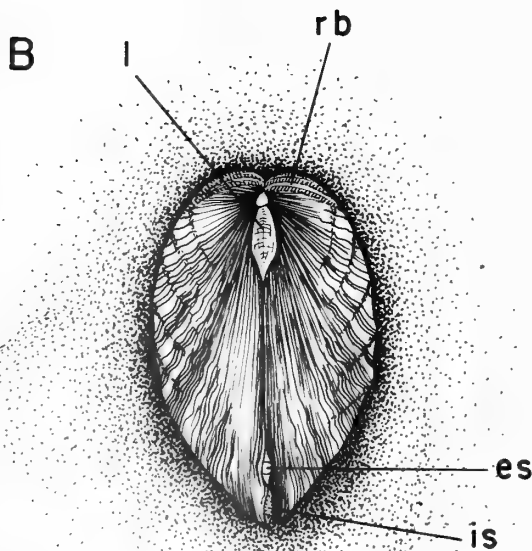
The goal of the present investigation was to study the structure, ciliary currents for feeding and digestion, and other functional adaptations of the subspecies *Castalia undosa undosa* Martens, 1827, providing information on the anatomy of the limnic fauna of South American bivalves and systematic data that may help distinguish species and subspecies of the genus *Castalia*.

MATERIALS AND METHODS

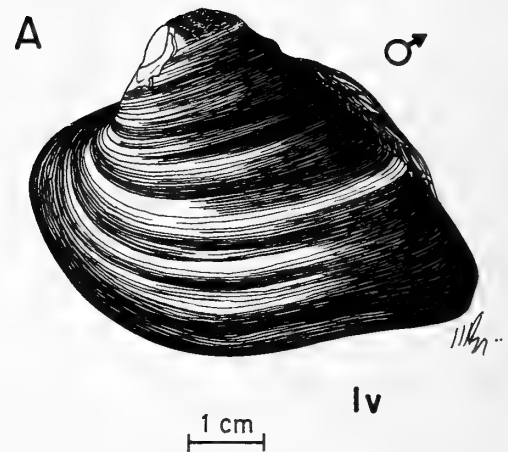
Living specimens of *Castalia undosa undosa* were collected in the Pardo River at the municipality of Ribeirão Preto (21°7'S, 47°45'W). Approximately 66 animals were captured throughout the study and carried to the laboratory, where they were kept alive in appropriate aquaria at 25°C. A few animals were anesthetized with magnesium chloride and then fixed in 10% formol, Bouin's, or 70% alcohol for morphological examination. To complement the anatomical studies, detailed drawings of the animals and of the arrangement of their inner organs were made using live, anesthetized specimens. The ciliary currents of the mantle, ctenidia, labial palps, and stomach were observed under a stereoscopic microscope using carmine or carborundum suspensions as indicators. Sections (7–10 µm thick) were



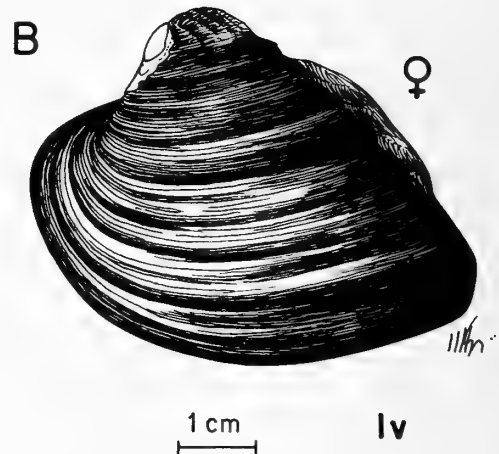
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1 cm



1 cm



1 cm

Figure 2

Castalia undosa undosa, external view of the left valve showing the lines of growth and ribs. A. Male. B. Female. lv, left valve.

prepared from structures fixed in Bouin's and stained with Ehrlich's hematoxylin and eosin.

HABITAT

According to BONETTO (1965), *Castalia undosa undosa* Martens, 1827, is found in the basin of the upper Paraná River, whereas the other subspecies, *C. undosa martensi* Ihering, 1891, is limited to the rivers of the South Atlantic coast of Brazil and to Uruguayan waterways.

Figure 1

Castalia undosa undosa, animals in their natural habitat. A. External view of the left side showing extended foot. B. Frontal view. es, excurrent siphon; is, incurrent siphon; l, ligament; rb, rib.

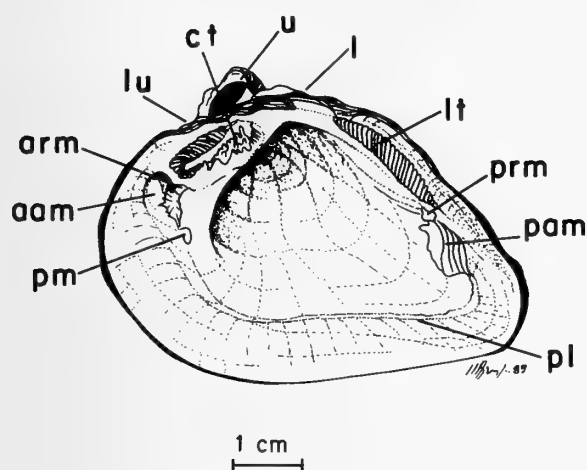


Figure 3

Castalia undosa undosa, internal view of the right valve, showing the muscles scars. aam, anterior adductor muscle; arm, anterior retractor muscle of foot; ct, cardinal tooth; l, ligament; lu, lunule; lt, lateral tooth; pam, posterior adductor muscle; pl, pallial line; pm, protractor muscle; prrm, posterior retractor muscle; u, umbo.

Castalia undosa undosa lives buried at sites with muddy substrata, generally under the shade of bushes and trees, or among the roots of aquatic plants. According to MANSUR (1972), *C. undosa martensi* preferentially lives near rushes in substrata where fine sand predominates.

Specimens of *Castalia undosa undosa* were collected at depths ranging from 0.70 cm to 1 m, in relatively calm waters. The animals burrow almost completely into the substratum (Figure 1A, B) and can be captured only by probing the river bottom with one's feet or hands. Several bivalve species were found at the Pardo River: *Diplodon rotundus gratus* Wagner, 1827; *Anodontites trapesialis* Lamarck, 1819; *A. trapezeus* Spix, 1827; and *A. crispatus* Orbigny, 1835. Two species of *Diplodon* and one of *Monocondylea* that could not be identified at the species level were also found. Large numbers of limnic acarids were observed in the branchiae of the animals studied; these probably belong to the genus *Unionicola*, subgenus *Pentatex*, and were mentioned by HEBLING (1976).

FUNCTIONAL ANATOMY

Shell

The shell of *Castalia undosa undosa* (Figure 2A, B) is subtriangular, equivalve, and inequilateral, with a prominent upper ridge that is truncated in the posterior region. The umbo (u) is prosogyrate with a worn periostracum. The lunule (Figure 3, lu) is easily visible, oval, and dark in color. The outer opisthodontic ligament (l) is also easily visible. In the dorsal area of the shell where the valves meet, and extending almost the entire length of the hinge, fused periostracal layers can be easily seen in specimens larger than 4 cm.

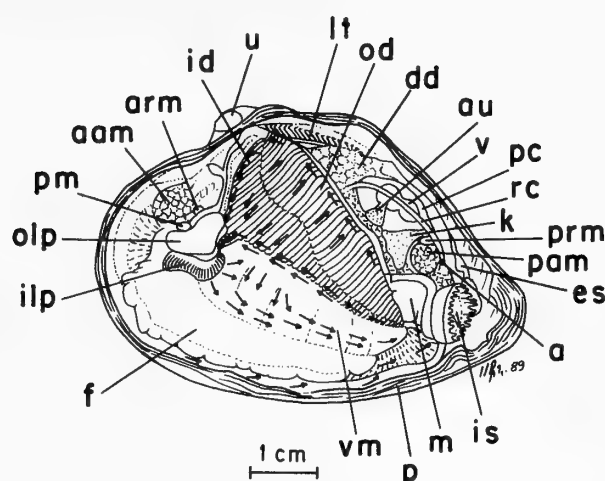


Figure 4

Castalia undosa undosa, organs and ciliary currents of mantle cavity after removal of left shell valve and mantle lobe. a, anus; aam, anterior adductor muscle; arm, anterior retractor muscle of foot; au, auricle; dd, digestive diverticula; es, excurrent siphon; f, foot; id, inner demibranch of ctenidia; ilp, inner labial palp; is, incurrent siphon; k, kidney; lt, lateral tooth; m, mantle; od, outer demibranch of ctenidia; olp, outer labial palp; p, periostracum; pam, posterior adductor muscle; pc, pericardium; pm, protractor muscle; prrm, posterior retractor muscle; rc, rectum; u, umbo; v, ventricle; vm, visceral mass.

The edges of the shell meet throughout their extension, leaving no opening.

The outer surfaces of specimens measuring up to 6 cm in length are sculptured with 8 to 13 ribs (Figure 1, rb) arranged almost in parallel but converging in the umbonal region. In larger specimens, the ribs are worn off, and only the growth lines are visible. In the posterior shell region there is marked sculpturing, with folds and nodules delimiting the anterior ribs. According to BONETTO (1965), these characteristics are distinct, indicating that this is a well-characterized subspecies.

The periostracum (Figure 4, p) of *Castalia undosa undosa* is dark brown in color, with marked abrasion in the umbonal region that is clearly visible in adult specimens. A notable characteristic of this species is that the shell has successive layers of periostracum and a thin underlying prismatic layer within the common mass of the inner calcareous layer of the valves. This characteristic was also observed by TAYLOR *et al.* (1969) in the Unionaceae and in the Hyriidae and Mycetopodidae collected during our studies. The umbonal abrasion is due to the velocity of the current passing over the animals, and to the nature of the substratum and the chemical composition of the water (BONETTO, 1963).

Castalia undosa undosa is sexually dimorphic, the males being distinguished by the posterior beak of the shell (Figure 2A, B), which is more tapered, and by having a depression in the posteroventral shell region.

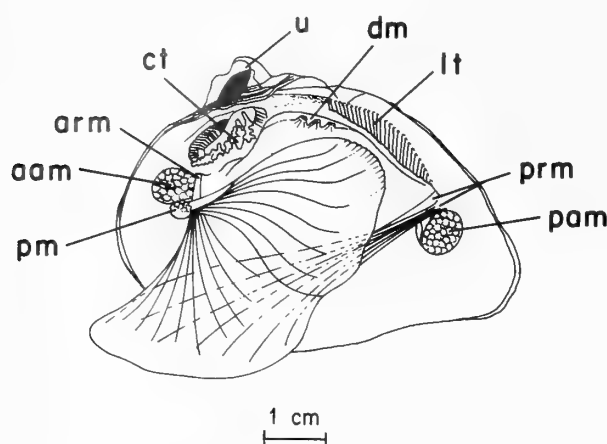


Figure 5

Castalia undosa undosa, lateral view of right valve musculature after removal of left valve, mantle, palps, and visceral mass. aam, anterior adductor muscle; arm, anterior retractor muscle; ct, cardinal tooth; dm, dorsal muscle; lt, lateral tooth; pam, posterior adductor muscle; pm, protractor muscle; prp, posterior retractor muscle; u, umbo.

The inner surface of the valves (Figure 3) is smooth and white in color. The hinge is well developed, with two cardinal teeth (ct) in each valve. The anterior cardinal tooth is larger than the posterior one, with several well-developed cusps. The outer and inner surfaces of the cardinal teeth of the left valve are crenulated, while on the right valve the crenulation is present only on the inner surface. In the right valve there is a lateral tooth with both surfaces showing crenulation, and in the left valve there is a facet of equal size whose inner surfaces are crenulated.

The pallial line (pl) starts below the scar of the anterior adductor muscle (aam) and extends posteriorly parallel to the shell margin, describing a curve that terminates at the base of the scar of the posterior adductor muscle (pam).

The scars of the adductor muscles vary in size according to specimen length, the posterior one being slightly longer than the anterior one. The anterior retractor muscle of the foot (arm) is located dorsolaterally to the anterior adductor muscle (aam), which is small and deep. Ventrally to the anterior adductor muscle is located the protractor muscle of the foot (pm), of slightly triangular contour and proportional in size to the anterior retractor muscle.

The scar of the posterior retractor muscle (prp), which is rounded in shape and similar in size to the anterior retractor muscle, is located dorsally to the posterior adductor muscle.

The dorsal, or elevator, muscles (Figure 5, dm) leave obvious scars in the valves, which, however, are difficult to see because of their location on the inner surface of the hinge in the umbonal cavity. The number of scars detected in *Castalia undosa undosa* ranged from 3 to 6. Elevator muscles have also been observed in *Leila blainvilleana* Ihering, 1890 (BONETTO, 1963), *Diplodon rotundus gratus*

(HEBLING & PENTEADO, 1974), and *Anodontites trapesialis* (HEBLING, 1976).

Mantle

By removing the animal's left valve (Figure 4) and the left mantle lobe, the pallial cavity is exposed. The three folds of the mantle margin are small; the medial one (sensory) and the outer one (secretory) are very close to one another. In the posterior region, the inner fold (muscular) bears two rows of small tentacles arranged at the entrance to the incurrent siphon. According to MORTON (1978), these tentacles have a sensory function and apparently take on the function of the middle fold. The mantle surface is uniformly cream colored, except for the region of the incurrent and excurrent siphons, where the mantle is dark cream colored.

The mantle lobes are usually free, except posteriorly where they are joined by an inner fold that separates the incurrent from the excurrent siphon and promotes the joining of the ctenidium through tissue fusion. Approximately 65% of the specimens studied had a second joining point that is below the incurrent opening and which separates the incurrent opening from the pedal opening.

The ciliary currents of the mantle surface are illustrated in Figure 11 and are similar to those described by HEBLING & PENTEADO (1974) for *Diplodon rotundus gratus*, and by HEBLING (1976) for *Anodontites trapesialis* and *A. trapezeus*.

Siphons

The siphons of *Castalia undosa undosa* are of type AII (YONGE, 1957), and are formed by the fusion of the inner fold of the mantle due to tissue joining. The incurrent siphon (is) is complete in most animals. However, incomplete siphons were observed in approximately 35% of the specimens. In *C. undosa martensi*, IHERING (1891) found that 1 of 8 specimens had an incomplete incurrent siphon, and MANSUR (1972) found the same phenomenon in 2 of 40 specimens.

On the inner margin of the incurrent siphon there are 23 to 85 simple, conically shaped tentacles, some of which may eventually bifurcate. They are arranged along two rows, an inner one and an outer one, the larger and darker tentacles being in the inner row.

In *Castalia undosa martensi* there are three rows of tentacles, varying in number from 80 to 180 (MANSUR, 1972).

The excurrent siphon, which is dark cream in color and has slightly undulating margins, has no tentacles. Wrinkles, spots, and small tubercles, varying in number from 1 to 8, may appear externally at the base of the siphon. Among the Hyriidae and the Mycetopodidae studied thus far, the occurrence of these tubercles has been reported only for *Castalia undosa martensi* by MANSUR (1972).

The sensitive siphon of *Castalia undosa undosa*, and other bivalves, which has been attributed by several investigators

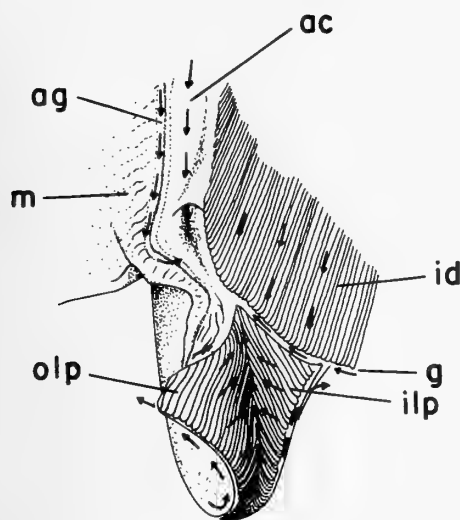


Figure 6

Castalia undosa undosa, labial palps of left side. Arrows show direction of ciliary currents. ac, anterior channel; ag, anterior groove of mantle; id, inner demibranch; g, marginal groove of inner demibranch; ilp, inner labial palp; m, mantle; olp, outer labial palp.

to the fact that these animals live in calm waters (OWEN, 1953; NARCHI, 1972a; HEBLING, 1976), was confirmed in the present study.

Muscles and Foot

In terms of muscle fiber arrangements and insertions on the valve, the musculature of *Castalia undosa undosa* (Figure 5) is similar to that of members of the Unionidae, Hyriidae, and Mycetopodidae (MANSUR, 1972; HEBLING & PENTEADO, 1974; HEBLING, 1976). The presence of dorsal muscles (dm), varying from 3 to 6 in number, is particularly clear in medium-sized and large specimens. These muscles were observed by BONETTO (1963) in *Leila blainvilleana* and by HEBLING (1976) in *Anodontites trapesialis*. According to HEBLING (1976), these muscles correspond to the elevator muscles of Brück described for *Anodonta cellensis*.

The foot (f) has no cilia, as was also observed in freshwater bivalves studied by other investigators, such as MANSUR (1972), HEBLING & PENTEADO (1974), and HEBLING (1976).

Mantle Cavity

Topography: The positions of the main organs of the mantle cavity are indicated in Figure 4. The visceral mass region is the first to be distinguished. This milky white and intensely ciliated region is responsible for rejectory

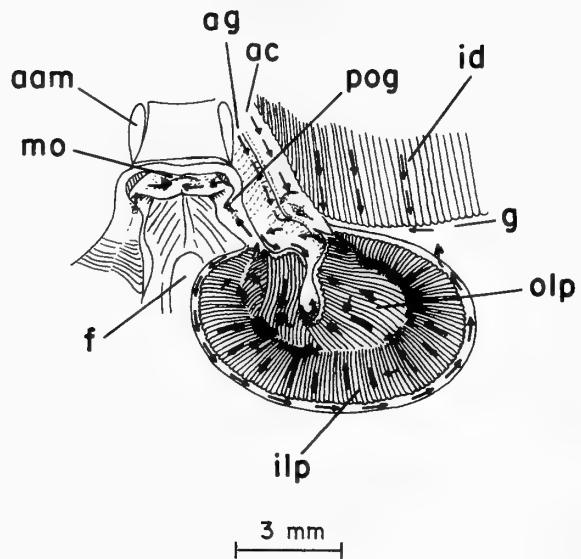


Figure 7

Castalia undosa undosa, structure and ciliary currents of ctenidial-labial palp junction as viewed from left side. aam, anterior adductor muscle; ac, anterior channel; ag, anterior groove of mantle; f, foot; g, marginal groove of inner demibranch; id, inner demibranch; ilp, inner labial palp; mo, mouth; olp, outer labial palp; pog, proximal oral groove.

currents that carry particles to the posterior region of the animal. Next are the foot, which is yellowish in color and has no cilia, and the ctenidia, which extend posteriorly from the umbral region to the base of the siphon process, where the process is fixed at the inner fold of the mantle. There is no supra-axial region. The mantle margins, observed next, may fuse or not at the base of the incurrent siphon, leaving a wide pedal opening that can be continuous or not with the incurrent siphon (is). Finally, there are the labial palps (ilp), which are large and slightly oval in shape.

Labial palps: In *Castalia undosa undosa*, the palps (Figure 6) are cream colored and symmetrical, with folded inner surfaces and smooth outer surfaces.

An area with no folds exists on the inner surfaces (Figure 7), both in the anterior and posterior regions. The anterior region is connected to the proximal oral groove (pog) and the posterior region to the anterior channel (ac). The food particles that reach the labial folds originate from the marginal food groove (g) of the inner demibranch, either from the anterior channel, which directs the particles originating from acceptance currents of the outer demibranch, or from the anterior mantle groove (ag), which sends the particles from the mantle to the dorsum of the outer labial palp. This last current was observed by MANSUR (1972) in *Castalia undosa martensi*. The mechanisms of particle screening and acceptance on the part of the labial palps are similar to those observed by HEBLING & PENTEADO (1974) and HEBLING (1976).

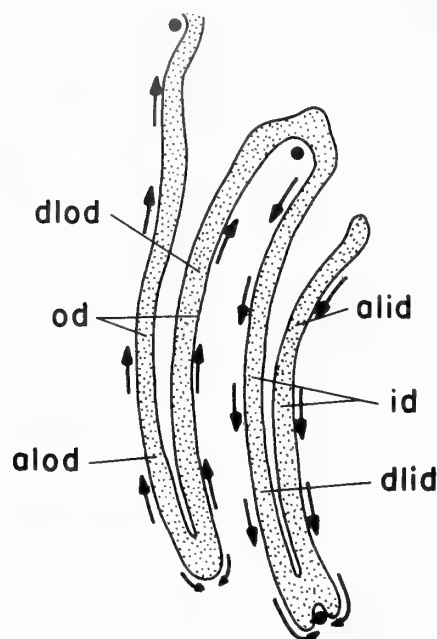


Figure 8

Castalia undosa undosa, diagrammatic vertical section through ctenidium to show direction of beat of frontal cilia. alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; id, inner demibranch; od, outer demibranch.

Ctenidia: The ctenidia of *Castalia undosa undosa* (Figure 8) are of type D (ATKINS, 1937), i.e., characterized by the absence of a marginal groove in the outer demibranch. According to ATKINS (1937), this type of ctenidium is characteristic of the Unionidae, though it has also been found in the Hyriidae (MANSUR, 1972; HEBLING & PENTEADO, 1974), Mycetopodidae (HEBLING, 1976), and Sphaeriidae (MANSUR & VEITENHEIMER, 1975). All indications are that the type D ctenidium is characteristic of freshwater bivalves.

The ctenidia of *Castalia undosa undosa* and *C. undosa martensi* originate in the subumbonal region and project toward the siphon region. They are arranged diagonally in relation to the visceral mass. The anterior filaments of the outer demibranch (Figure 4, od) are smaller than those of the inner demibranch and increase gradually in size posteriorly (Figure 4).

The inner demibranch (id) grows anteriorly in relation to the mantle and visceral mass, forming a wide and easily visible anterior channel (ac) that ends in the dorsal region of the labial palps (Figures 6, 7). The demibranchs are formed by shallow folds, with filaments varying in number from 17 to 32 in the ascending lamella (alod) and from 16 to 29 in the descending lamella (dlod) of the outer demibranch (od). In the inner demibranch (id), the number

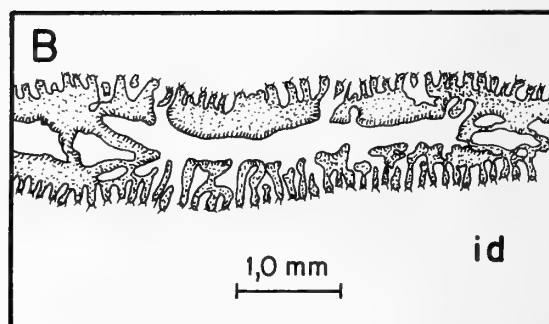
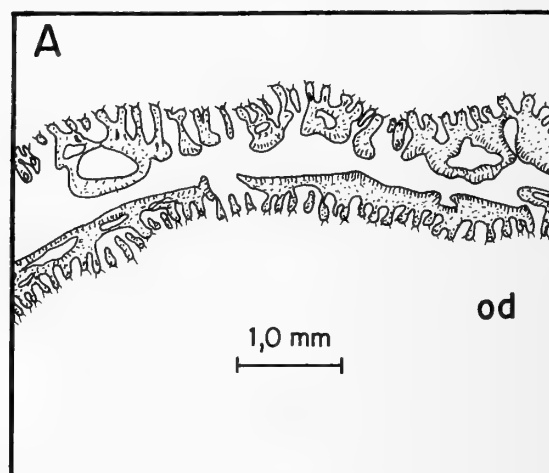


Figure 9

Castalia undosa undosa, transverse sections through a portion of outer (A) and inner (B) demibranchs showing arrangement of folds and filaments. id, inner demibranch; od, outer demibranch.

of filaments varies from 26 to 39 in the descending lamella (dlid) and from 22 to 40 in the ascending lamella (alid) (Figures 8, 9A, B).

In female specimens and in the few living hermaphrodites, the characteristic marsupium of freshwater bivalves is detected in the inner demibranch, but is visible only when the animals are in the reproductive cycle.

The ciliation of *Castalia undosa undosa* (Figure 10A, B) is similar to that of *Diplodon rotundus gratus* (HEBLING & PENTEADO, 1974), *Anodontites trapezeus*, and *A. trapesialis* (HEBLING, 1976).

The frontal cilia (fc) are approximately $3.3 \mu\text{m}$ long, and the terminal cilia (tc) are $6.6 \mu\text{m}$ long in the inner demibranch and $3.3 \mu\text{m}$ in the outer demibranch. The eulaterofrontal cilia (lfc) are $13.4 \mu\text{m}$ long, and the lateral cilia (lc) $9.8 \mu\text{m}$. The ciliary currents observed on the branchial surface are illustrated in Figure 8.

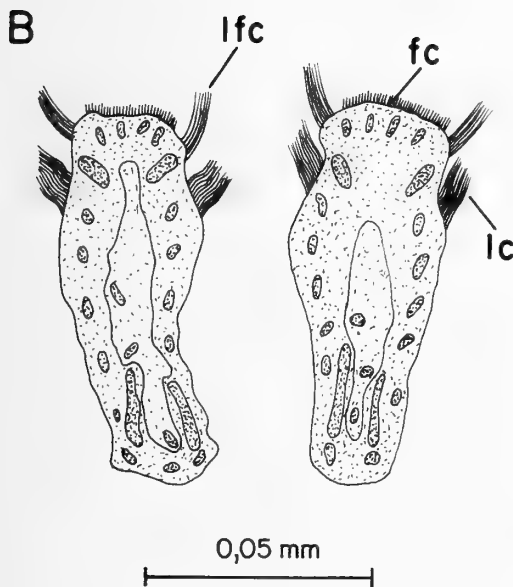
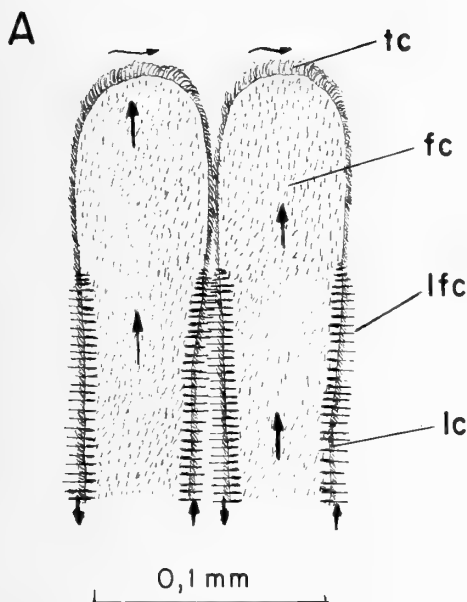


Figure 10

Castalia undosa undosa. A. Cilia on outer surface of inner demi-branch. B. Transverse section of two filaments of inner demi-branch to show cilia. Arrows indicate direction of ciliary currents, including the oral one. fc, frontal cilia; lc, lateral cilia; lfc, lateral frontal cilia; tc, terminal cilia.

Ciliary Currents of the Mantle

The ciliary currents of the inner mantle surface (Figure 11) run in an anteroventral direction up to the ventral region of the anterior adductor muscle. This current is

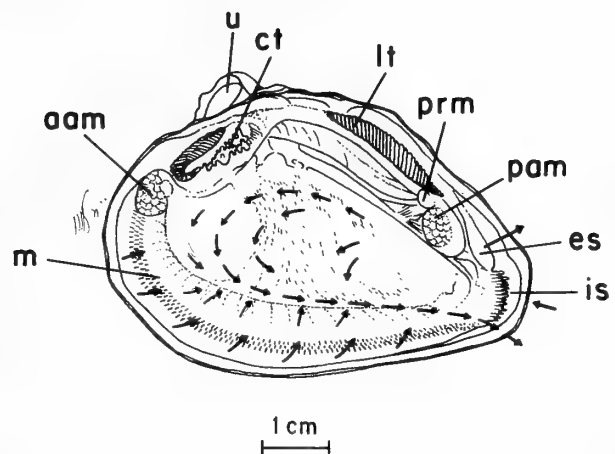


Figure 11

Castalia undosa undosa, inner surface of right mantle lobe to show ciliary cleansing currents. aam, adductor anterior muscle; ct, cardinal tooth; es, excurrent siphon; is, incurrent siphon; lt, lateral tooth; m, mantle; pam, posterior adductor muscle; prm, posterior retractor muscle; u, umbo.

associated with the rejectory tract of the mantle lobe, which runs in a posterior direction. This tract also receives particles from the pedal opening. The rejectory tract originates in the ventral region of the anterior adductor muscle where the labial palps are intensely active in screening and rejecting particles that fall in this region. The tracts of the two mantle lobes join at the bases of the incurrent siphon, where pseudofeces are periodically eliminated. Similar currents occur in members of the Unionidae (KELLOGG, 1915), Hyriidae (HEBLING & PENTEADO, 1974), and Mycetopodidae (HEBLING, 1976).

Ciliary Currents in the Visceral Mass

The ciliary currents in the dorsal region of the visceral mass run in a ventral direction. At the border between the visceral mass and the foot there is a rejectory tract that sends the particles rejected by the labial palps and inner demibranch to the posterior region (Figure 4). The currents running in the ventral direction join those of the rejectory tract and so the rejected particles are sent toward the posterior end of the visceral mass where they fall in the rejectory tract of the mantle. Similar rejectory tracts have been detected in the visceral mass of marine bivalves such as the Petricolidae (NARCHI, 1975; MORTON, 1978).

Alimentary Canal

The general topography of the digestive tract is illustrated in Figure 12.

The mouth (mo) is located in the posteroventral region of the anterior adductor muscle. The mouth is followed by an esophagus (oe) whose inner wall has grooves and folds that are interrupted at the entrance to the stomach by a

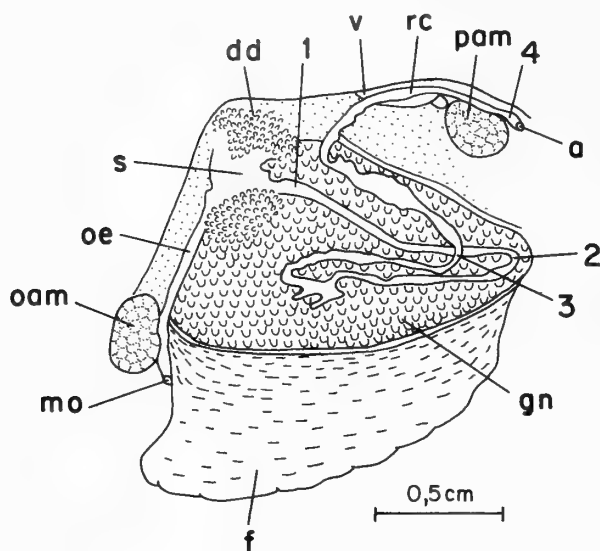


Figure 12

Castalia undosa undosa, alimentary canal seen from left side. The numerals 1, 2, 3, and 4 denote major subdivisions in the gut posterior to the stomach. a, anus; aam, anterior adductor muscle; dd, digestive diverticula; f, foot; gn, gonad; mo, mouth; oe, esophagus; pam, posterior adductor muscle; rc, rectum; s, stomach; v, ventricle.

transverse ridge (Figure 13, rm). The stomach is located in the anterodorsal region of the visceral mass and is enveloped by digestive diverticula.

The stomach of *Castalia undosa undosa* is of type IV (PURCHON, 1958), as it is in the Unionidae (GRAHAM, 1949; PURCHON, 1958; DINAMANI, 1967), Mycetopodidae (HEBLING, 1976; VEITENHEIMER & MANSUR, 1978), and Hyriidae (MANSUR, 1972; HEBLING & PENTEADO, 1974; and MANSUR & ANFLOR, 1981).

The general morphology of the stomach, the complexity of the ciliary currents and screening areas, and the conjugated intestinal and crystalline style sac (ss) apertures (Figure 13) are similar to those observed in the bivalve families studied by the investigators cited above.

The gut of *Castalia undosa undosa* is divided into three regions. The aperture of the style sac is associated with the first region, which extends through a posterior loop to the opening of the stomach (Figure 12, 1-2). The second region (2-3) consists of two loops of mid-gut, the lumen of which has a conspicuous typhlosole. The third region (3-4) is an extensive loop terminating in the anus. The rectum occupies a reasonably large area of the visceral mass, and has a developed typhlosole. The arrangement of the gut in the visceral mass follows the pattern of Hyriidae such as *C. undosa martensi* (MANSUR, 1972), *Diplodon rotundus gratus* (HEBLING & PENTEADO, 1974), *D. charruanus* Orbigny, 1835, and *D. pilsbryi* Marshall, 1928 (MANSUR & ANFLOR, 1981).

Pericardium, Heart, Kidney, and Gonads

The pericardium is a wide structure located below the posterodorsal region of the shell. The heart consists of a ventricle, two auricles, and an aortic bulb. Brown tissue on the anterior wall of the pericardium denotes the presence of the pericardial gland, which is similar to that of *Anodonta* (WHITE, 1942). The rectum crosses the entire length of the ventricle, entering it in the usual manner, i.e., ventrally to the anterior aorta.

The kidney extends posteroventrally to the pericardium and is essentially similar to that of *Anodonta* (WHITE, 1942; YONGE, 1978).

In *Castalia undosa undosa*, hermaphroditism is rare, and was present in only 2 of 66 individuals studied. The male or female follicles are arranged along the entire visceral mass that envelops the digestive tract.

DISCUSSION

Studies of the functional anatomy of *Castalia undosa undosa* have revealed the existence of anatomical similarities among the Hyriidae, Mycetopodidae, and Unionidae studied by different investigators.

Castalia undosa undosa lives in muddy substrata similar to those inhabited by *C. inflata*, but differing in this respect from *C. undosa martensi* (MANSUR, 1972) and *C. psammoica* (BONETTO, 1961), which live on sandy bottoms.

In general, studies on freshwater bivalves have shown few special adaptations to the habit of living close to the surface in relatively soft substrata and feeding on particles in suspension. This fact was also pointed out by ANSELL (1961) for marine bivalves. According to OWEN (1953), many of the adaptations of bivalves that filter particles in suspension (Solenidae and Myiidae) are correlated with their habit of burrowing deeply, with a consequent loss of horizontal mobility.

The ability to burrow into soft substrata and to occupy the same site for long periods of time, which is true for *Castalia undosa undosa* as well as *Anodontites trapesialis* (HEBLING, 1976), may be associated with the lack of functionality of the elevator muscles, which are underdeveloped in these animals and absent in others, such as *A. trapezeus* (HEBLING, 1976). NARCHI (1978) proposed that functional elevator muscles help the animals burrow in compacted substrata, as is the case with *Donax*, which is frequently uncovered by the action of waves.

Castalia undosa undosa has relatively simple tentacles. Studying marine bivalves, NARCHI (1972b) attributed the simplicity of the siphons of *Anomalocardia* to the fact that the animals live in calm waters and feed on particles in suspension. Similarly, *C. undosa undosa* lives in calm waters and feeds on suspended particles.

According to BONETTO (1961), the presence of a muscle septum separating the pedal orifice from the incurrent orifice is an almost constant feature in the genus *Castalia*. The absence of a muscular septum in *C. undosa undosa* is

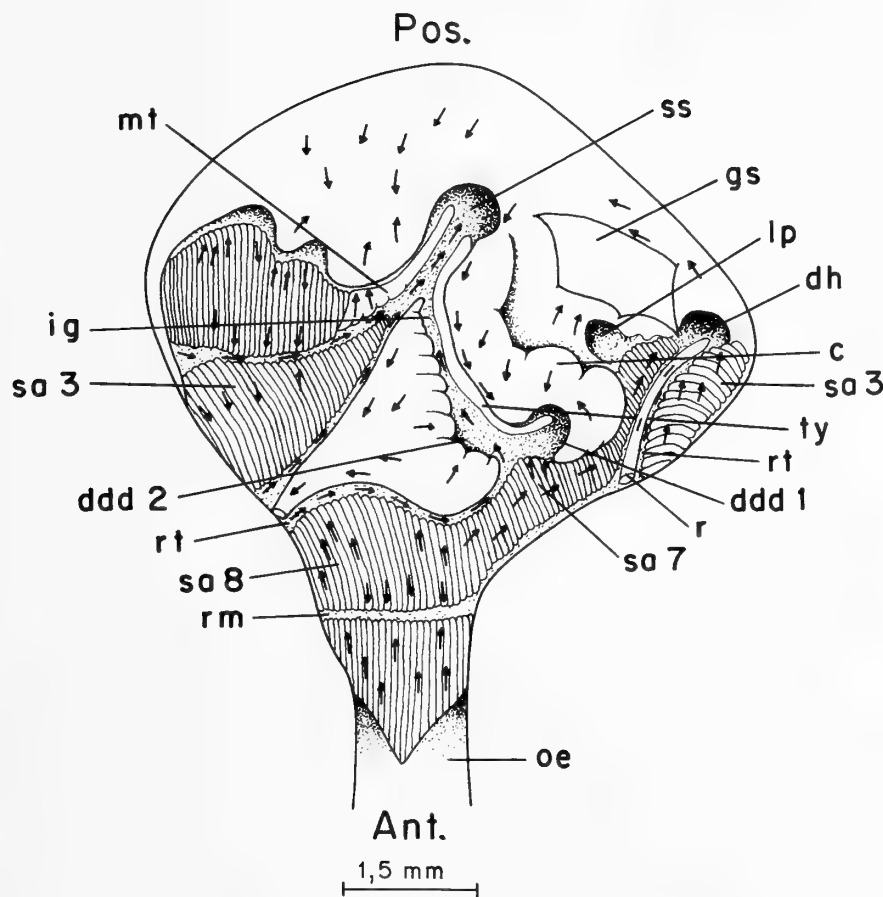


Figure 13

Castalia undosa undosa, structure of interior of stomach opened by middorsal incision. Arrows show direction of ciliary currents. ant, anterior; c, conical protuberance of floor of stomach; ddd1, orifice of left duct of digestive diverticula; ddd2, orifice of right duct of digestive diverticula; dh, dorsal hood; gs, gastric shield; ig, intestinal groove; lp, left pouch; mt, minor typhlosole; oe, esophagus; pos, posterior; r, ridge passing from esophageal orifice over roof of dorsal hood; rm, transverse ridge; rt, ciliated rejectory tract; sa3, principal sorting area of dorsal hood; sa7, sorting area below esophageal orifice; sa8, sorting area on anterior roof of stomach; ss, orifice of style sac and mid-gut; ty, major typhlosole.

relatively frequent (35%) when compared with other species in the genus, for which the highest frequency otherwise recorded was 5%, for *C. undosa martensi* (MANSUR, 1972).

The branchial cilia (lateral, frontal, terminal, and eu-laterofrontal cilia) of *Castalia undosa undosa* are small when compared with those of the marine bivalves living in turbulent waters studied by NARCHI (1974). However, they are similar to those of freshwater bivalves living in the same type of environment, such as *Anodontites trapezeus* and *A. trapesialis* (HEBLING, 1976), and they are proportionally smaller when compared with the cilia of *Diplodon rotundus gratus* (HEBLING & PENTEADO, 1974) which lives in sandy substrata. Thus, the presence of relatively short cilia may be associated with the animals' habit of living in muddy environments with large amounts of very fine particles in suspension, such as silt, clay, and monocellular phytoplankton.

Another adaptation that can be attributed to a muddy type of environment is the marked development of the labial palps, which, according to YONGE (1949), is common in animals burrowing in muddy substrata. According to HEBLING (1976), the complexity of the ciliary currents observed in the palps leads to greater efficiency in particle selection.

The stomach of *Castalia undosa undosa* and most freshwater bivalves is type IV (PURCHON, 1958). Some freshwater bivalve genera such as *Dreissena* and *Corbicula* have a type V stomach (PURCHON, 1960). This uniformity of structures and ciliary currents can be seen in the studies conducted by GRAHAM (1949), PURCHON (1958), DINAMANI (1967), HEBLING & PENTEADO (1974), HEBLING (1976), and VEITENHEIMER & MANSUR (1978).

According to HEBLING (1976), the anatomical uniformity of freshwater bivalves is due to convergent adaptation,

where by the different species have only a few points of difference and are practically identical in general terms.

The three regions of the gut, with the typhlosole reducing the lumen and persisting throughout the length of the gut, are characteristics comparable to those detected in the Etheriidae by YONGE (1978), who considers this characteristic similar to that of the Unionidae studied by JEGLA & GREENBERG (1968). The configuration of the gut may possibly be a specific characteristic of the Hyriidae, as shown by MANSUR (1972, 1973), HEBLING & PENTEADO (1974) and the present study. More data, however, are needed to substantiate this statement.

In *Castalia undosa undosa*, hermaphroditism is extremely rare and a clear sexual dimorphism occurs in the shell of the males; in males, the tip angle is smaller and the shell has a slight depression in the posteroventral region. Among the Hyriidae and Mycetopodidae studied, sexual dimorphism occurs only in *C. undosa undosa*.

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Commensals Associated with *Xenophora (Onustus) longleyi* Bartsch (Mollusca: Gastropoda) in the Gulf of Mexico and Caribbean Sea

by

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Abstract. Forty-seven specimens of *Xenophora (Onustus) longleyi* from 11 locations in the Gulf of Mexico and Caribbean Sea were examined for commensals. Commensal type and frequency are described among five size classes of *X. longleyi*. In addition, egg cases containing well-developed larvae are described, and may be the first reported for any species within the Xenophoridae.

INTRODUCTION

Xenophora (Onustus) longleyi Bartsch, 1931, is a relatively common deep-water mesogastropod occurring in soft sediments in the western Atlantic (PONDER, 1983). One of the largest in the family Xenophoridae, this species is known to have many commensals, including tube-building polychaete worms and *Epizoanthus* (TAKEDA & OKUTANI, 1983). However, no study, descriptive or otherwise, has been undertaken on the relationship between *X. longleyi* and its commensals.

The biology of the deep-water Xenophoridae is poorly known, although some work has been done on a few of the shallow-water species (CROZIER, 1919; MORTON, 1958; SHANK, 1969; BERG, 1975). Gut content analysis suggest they are detritivores, although *Xenophora (Onustus) exuta* was found to feed selectively on foraminiferans (PONDER, 1983). Their general life history suggests they are well adapted to eluding detection by predators (ST. JEAN, 1977). The exterior of the shell is usually well camouflaged with attached debris, although deeper-water species living on soft, uniform bottoms are thought to have little attached material since visual predation is no longer relevant (PONDER, 1983).

Xenophora longleyi is known to have commensals living on the exterior, on the base, and within the umbilicus (TAKEDA & OKUTANI, 1983). The purpose of this paper is to describe the types of commensals and determine whether there is a relationship between shell size and

commensal frequency on 47 specimens of *X. longleyi* from 11 stations in the Gulf of Mexico and Caribbean Sea.

MATERIALS AND METHODS

Twenty-six specimens of *Xenophora longleyi* were obtained from a survey on the fishery potential of the megalops shrimp, *Penaeopsis serrata*, from six stations in the north and northwestern Gulf of Mexico (Figure 1). All of these stations were characterized by soft sediments with depths ranging from 311 to 704 m. All specimens from this fishery project have been deposited at the California Academy of Science, San Francisco. The remaining 21 specimens were examined from the Texas A&M Oceanography Collection (TAMOC 4-0389, 4-1224, 4-1755, 4-1756, 4-1757) collected from stations located in the southwestern Gulf of Mexico and Caribbean Sea in depths ranging from 457 to 823 m (Figure 1).

Shell height was measured from the apex to the lower margin of the aperture of each shell. Basal diameter was recorded as the greatest distance between the sutures along the shell base. The relationship of shell height to basal diameter was examined using linear regression.

The basal diameter was used as the most consistent measure of shell size, since the apex of some of the larger specimens was eroded. The number and type of commensals were recorded for each specimen, and frequencies of these values were established by partitioning the basal diameter values into discrete size classes (2.0-2.9 cm, 3.0-

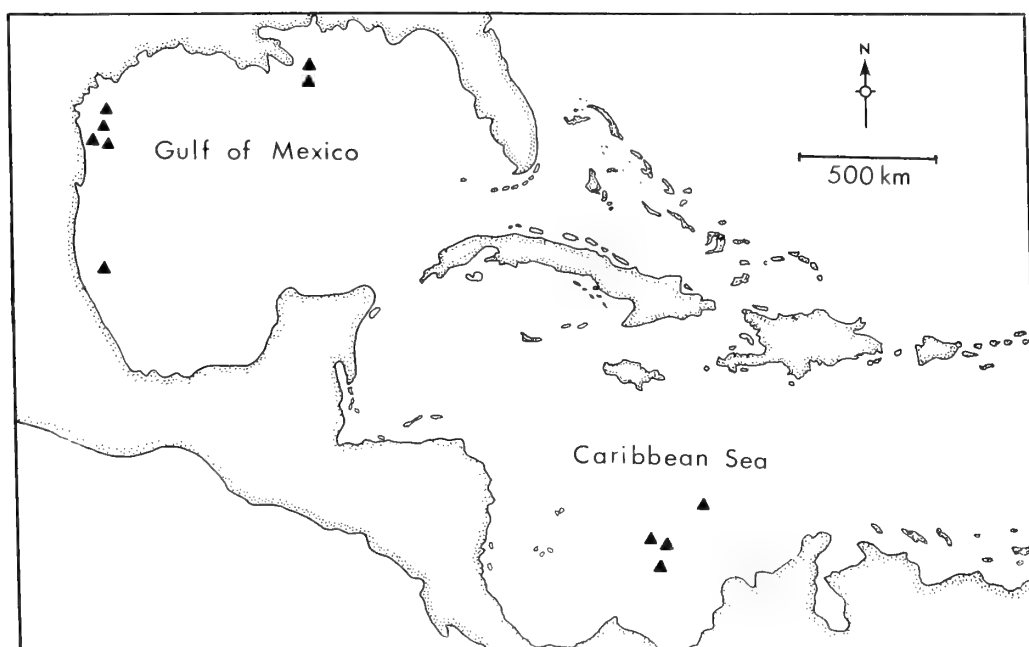


Figure 1

Eleven locations where 47 specimens of *Xenophora (Onustus) longleyi* were obtained.

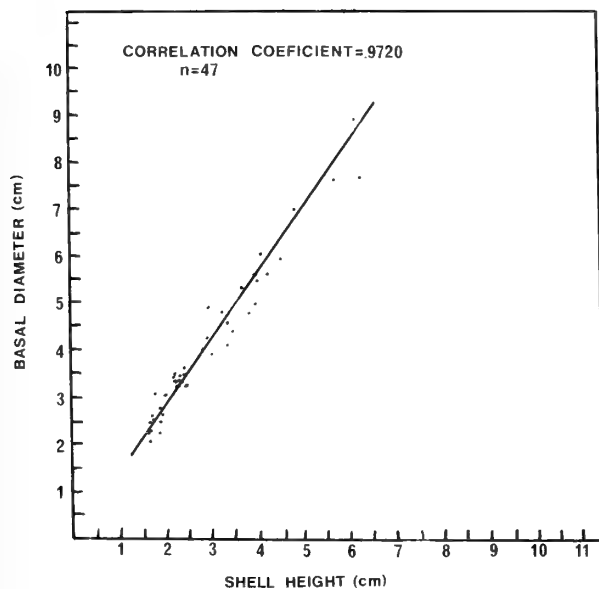


Figure 2

Basal diameter versus shell height in 47 specimens of *Xenophora (Onustus) longleyi*. These two parameters show a strong positive correlation: $r = 0.9720$ with a slope of 1.2769, and variance of 2.1×10^{-3} .

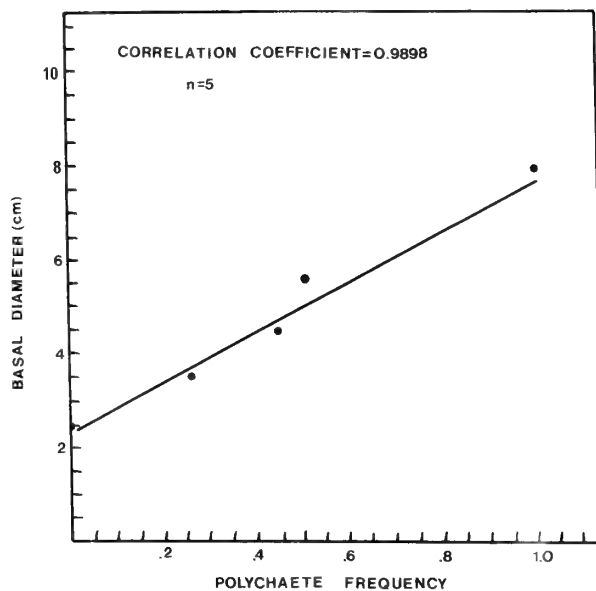


Figure 3

Basal diameter versus the commensal polychaete frequency observed in 47 specimens of *Xenophora (Onustus) longleyi*. These two parameters are positively correlated: $r = 0.9898$ with a slope of 5.56, and a variance of 2.93.

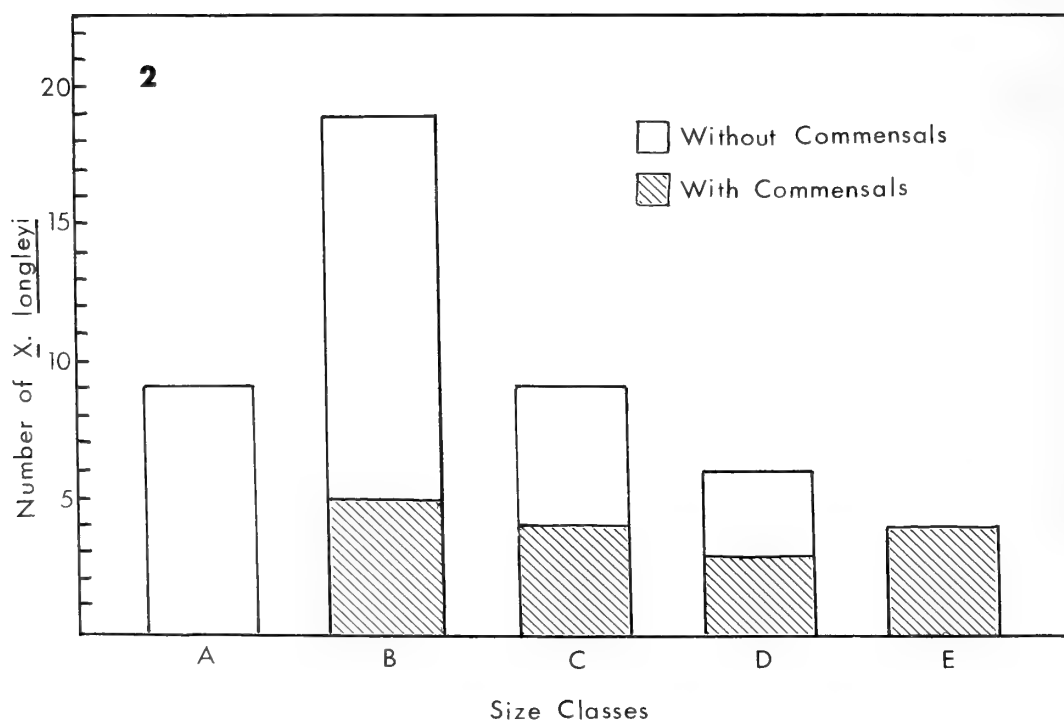
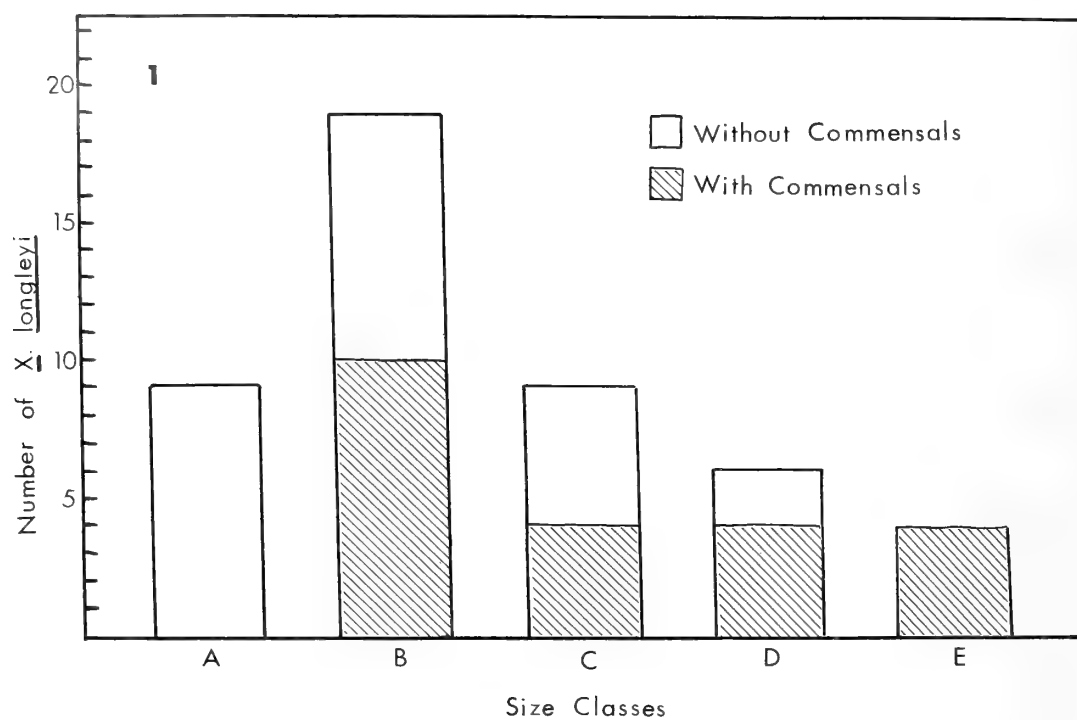
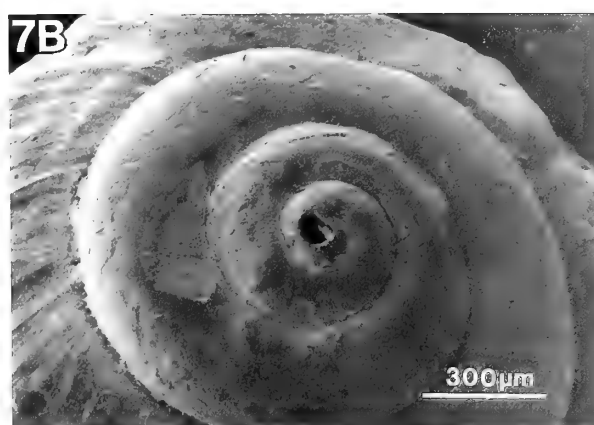
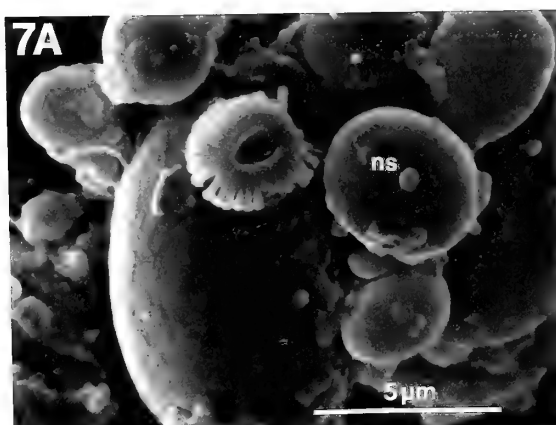
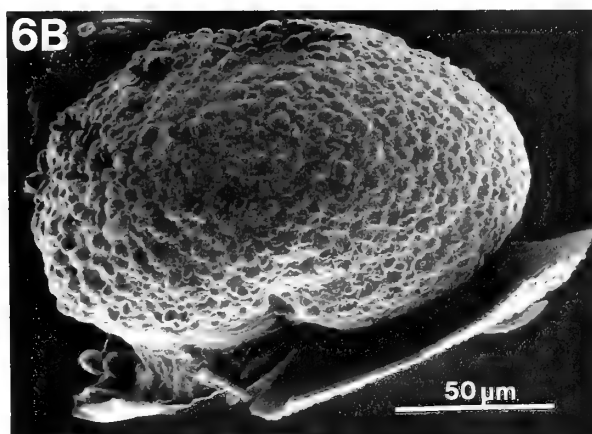
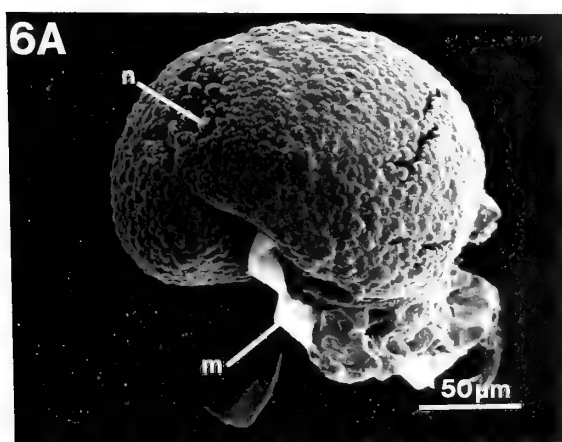
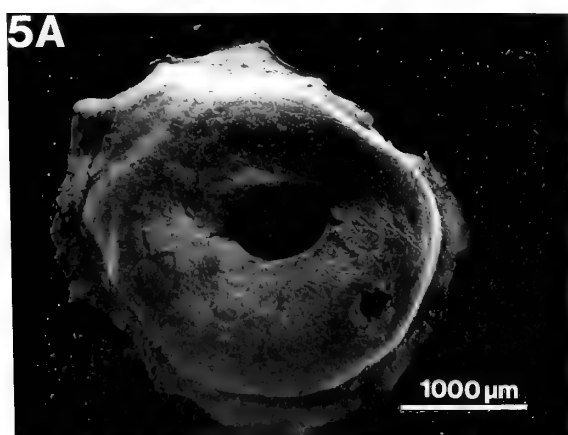


Figure 4

Size-class frequency distribution of *Xenophora (Onustus) longleyi*. The proportion of specimens with commensals (1). The proportion of specimens with commensal polychaetes living in the umbilicus (2). Key: A, 2.0–2.9 cm; B, 3.0–3.9 cm; C, 4.0–4.9 cm; D, 5.0–5.9 cm; E, >6.0 cm.



Explanation of Figures 5 to 7

Figure 5. An egg case found just outside the aperture of *Xenophora (Onustus) longleyi*. A. Egg case. B. Magnified view of egg case membrane.

Figure 6. Developing larvae from the egg case in Figure 5. A and B. Two different views. Key: n, embryonic shell nodule; m, embryonic membrane.

Figure 7. Protoconch of a juvenile specimen of *Xenophora (Onustus) longleyi*. A. Calcareous nodules observed along the suture line of the protoconch of the same size and shape as nodules from the embryonic shell shown in Figure 6. B. Slightly eroded protoconch. Key: ns, suture nodule.

3.9 cm, 4.0–4.9 cm, 5.0–5.9 cm, >6.0 cm). Shell size classes and commensal frequencies were related using linear regression analysis of basal diameter versus commensal frequency. Observations of some egg cases containing larvae, and of the protoconch of a juvenile *Xenophora longleyi* were made using SEM techniques.

RESULTS

Basal diameter ranged from 2.2 to 8.6 cm, and shell height ranged from 1.7 to 6.1 cm. Basal diameter was strongly correlated with shell height (Student's *t*-tests of $r \neq 0$; $P < 0.0001$). The slope was 1.2769 with a variance of 2.1×10^{-3} (Figure 2).

The numbers and types of commensals found on the specimens are summarized in Table 1, and included representatives from the phyla Cnidaria (sea anemones and zoanthids), Annelida (polychaete worms), and Arthropoda (barnacles). The five shell size classes did not correlate with the total commensal frequency (Student's *t*-test of $r \neq 0$; $P < 0.1$). The slope was 5.56 with a variance of 2.93 (Figure 3). A more descriptive frequency distribution shows the proportion of specimens with commensals within each of the size classes (Figure 4).

Fourteen gastropod egg cases containing shelled larvae were found on the shell base near the aperture of one specimen from the northwestern Gulf of Mexico taken during the month of June (Figures 5, 6). Twenty-two other egg cases were found on the exterior of eight specimens taken from three out of the four Caribbean locations during the month of July. These 22 egg cases could not be identified, but all were identical and appeared to have a single large trochophore larva surrounded by light colored yolk material.

DISCUSSION

The eunicid polychaetes are usually restricted to hard substrates, and are commonly carnivores, although some scavengers and detritivores are known (FAUCHALD, 1977). The eunicids found living on *Xenophora longleyi* build tough parchment-like tubes within the umbilicus of this species. The single scale worm observed could not be identified beyond the family Polynoidae because all but one of the elytra were missing. However, scale worms are typically common in deep-water areas (LEVENSTEIN, 1984). All of these commensals are likely to benefit when food is stirred or uncovered from the sediment by foraging or locomotor activity of *X. longleyi*. Although the sediment may be disturbed within the confines of the wide peripheral flange when the animal is foraging from its retracted position, most of the disturbance probably occurs when the animal exhibits its peculiar hopping motion during the locomotion described by PONDER (1983).

Hard substrate is a scarce resource for deep-sea sessile invertebrates along the deep-water continental shelf where

Table 1

The types and numbers of commensals found on 47 specimens of *Xenophora (Onustus) longleyi*.

	Number of commensals	Number of <i>X. longleyi</i>
Phylum Cnidaria		
<i>Epizoanthus</i> sp.	8	8
Actinaria sp.	9	5
Phylum Annelida		
<i>Eunice aphoditois</i>	12	12
<i>Eunice</i> (other)	3	3
Polynoidae sp.	1	1
Phylum Arthropoda		
<i>Verruca floridiana</i>	9	2
<i>Acroscapellum intonsum</i>	3	1
Totals	45	22

Xenophora longleyi was found in this study (HOLLAND *et al.* 1980). As a result, this species provides attachment space for larvae that might otherwise have little chance for survival. Some of the commensals also derive protection from the shell. Polychaetes are well protected by living in the umbilicus of the shell, while zoanthids are well protected where they attach along the base of the shell within the confines of the wide peripheral flange.

No strong correlation could be found between shell size classes and commensal frequency, primarily because the sample size was too low to generate a more accurate frequency distribution with a greater number of size classes. Clearly, however, commensals are absent or in lower proportion in smaller specimens (Figure 4).

The shell of *Xenophora longleyi* provides, in addition to a hard substrate for commensals, hard substrate on which invertebrates can lay eggs. The eggs found on the exterior of the Caribbean shells were all the same. This is not surprising since the eggs were found on specimens from the same general region at the same time of year. The molluscan egg cases (Figure 5) found on the specimen from the Gulf of Mexico may be of more significance. There are no known records of the spawn or larvae for any *Xenophora* species (PONDER, 1983). However, these egg cases could possibly have been laid by *X. longleyi*. It is unlikely that another mollusk would intrude to within the protective boundary of the peripheral flange near the aperture unless it was a predator. The egg cases were laid just outside the aperture. Each of the larvae within the egg cases was enclosed in a thin membrane and had a shell closely resembling the beginning of the protoconch shown for *X. longleyi* (Figures 6, 7). The calcareous nodules that constitute the embryonic shell were observed to be the same size and shape as those observed along the suture line of the protoconch of *X. longleyi*.

ACKNOWLEDGMENTS

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Four New Pseudococculinid Limpets Collected by the Deep-Submersible *Alvin* in the Eastern Pacific

by

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Abstract. Four new species of Pseudococculinidae collected with the deep-submersible *Alvin* are described. One species represents a new monotypic genus, *Punctabyssia*, and two represent new subgenera: *Dictyabyssia* (of *Caymanabyssia* Moskalév, 1976) and *Gordabyssia* (of *Amphiplica* Haszprunar 1988). New species are: *Punctabyssia tibbettsi* and *Caymanabyssia* (*Dictyabyssia*) *fosteri*, both from the same piece of wood at abyssal depths on the East Pacific Rise Axis near 12°N, and two from abyssal depths on the Gorda Ridge off northern California, *Caymanabyssia* (*Caymanabyssia*) *vandoverae* and *Amphiplica* (*Gordabyssia*) *gordensis*. The latter is the first member of the family to be recovered from sulfide crust in the hydrothermal-vent habitat. New character states for the radula and protoconch are defined for the new genus *Punctabyssia*.

INTRODUCTION

The cocculiniform limpets include a number of deep-sea families in which there is an association with biogenic substrates (for review see HASZPRUNAR, 1988b). Until recently the only method by which these limpets have been recovered has been by chance trawling of pieces of wood or other biogenic substrates. Records of cocculiniform limpets are so infrequently obtained that many species remain known from a single station. Such a sparsity of records indicates that our knowledge of the distribution of these species is very incomplete and that additional new species are likely to be discovered.

A more direct approach to sampling the widely scattered wood or bone "islands" (TURNER, 1978) is now possible with the deployment of deep-submersible research submarines. The four pseudococculinid limpets described here were collected by using the deep-submersible *Alvin* of the Woods Hole Oceanographic Institution. Although the objective of each dive was the exploration of hydrothermal-vent fields, three of the four species were taken on wood outside the influence of hydrothermal activity.

Two species were found on the same piece of wood recovered from the ridge axis of the East Pacific Rise near 12°N. One represents a monotypic new genus, and the other a new subgenus, which has a congener from abyssal depths near New Zealand.

Two species are added from explorations of the *Alvin* on the Gorda Ridge, one from wood not under the influence

of hydrothermal vents, and another from sulfide crust produced by hydrothermal vents. The latter species represents a new monotypic subgenus and is the first member of the family restricted to the hydrothermal-vent habitat.

Recent work on the systematics and anatomy of the pseudococculinid limpets (MOSKALEV, 1976; HICKMAN, 1983; MARSHALL, 1986; HASZPRUNAR, 1988a; McLEAN, 1988) makes it possible to establish the taxonomic placement of the four new species treated here, and to justify the proposal of new generic and subgeneric taxa.

The new species described here introduce new character states for the family Pseudococculinidae and contribute to the understanding of relationships of genera within the family. The broader implications for classification are summarized in the discussion.

MATERIALS AND METHODS

Limpet specimens were collected on wood or other substrate samples with the mechanical arm of the deep-submersible *Alvin*. Material was preserved on reaching the surface, fixed in buffered formalin, and transferred to 70% alcohol. Sorting was accomplished at Woods Hole Oceanographic Institution, following which the specimens were forwarded to me.

Radulae were extracted from preserved specimens after dissolution of tissues in 10% NaOH, washed in water, air dried, and coated with gold or gold-palladium for examination with SEM. Protoconchs and juvenile shells were

examined with SEM. Protoconch lengths were taken directly from scale indications for the SEM micrographs.

Institutions mentioned in the text are abbreviated as follows: LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, Washington, D.C.

Suborder Cocculiniformia Haszprunar, 1987

Superfamily LEPETETELLACEA Dall, 1881

Family PSEUDOCOCCULINIDAE Hickman, 1983

Punctabyssia McLean, gen. nov.

Type species: *P. tibbettsi* McLean, sp. nov.

Diagnosis: Shell thin and translucent; protoconch with tightly spaced pits in longitudinal rows; teleoconch sculpture of fine concentric ridges with larger pits in interspaces. Eyes lacking, right cephalic tentacle slightly larger than left; gill leaflets present on right side only; epipodial tentacles a single posterior pair. Rachidian tooth large and quadrangular, uncusped; cusp of first lateral with fine serrations; upper shaft and cusp of second lateral fused with that of first lateral; third and fourth laterals with long beaklike cusps; fifth lateral reduced to stubby base; marginals similar in size.

Remarks: The protoconch sculpture of *Punctabyssia* is unique in having pits in rows. *Punctabyssia* is also unique in the serration on the first lateral and in the fusion between the cusps of the first and second laterals. Punctations on the protoconch are otherwise known only in *Tentaoculus* Moskalev, 1976. As diagnosed by MARSHALL (1986), *Tentaoculus* differs in having the protoconch pits in irregular order, in having a tapered, cusped rachidian, a strongly developed fifth lateral, having eyes, and occurring at bathyal rather than abyssal depths.

Etymology: The name derives from the Latin noun *punctura*, hole, with reference to the punctate sculpture of both protoconch and teleoconch, combined with the word-ending first used by MOSKALEV (1976) for genera related to *Pseudococculina*.

Punctabyssia tibbettsi McLean, sp. nov.

(Figures 1–8)

Description: Shell (Figures 1–3, 6) of medium size for family (maximum length 5.0 mm), translucent; periostracum thin, smooth. Height low, that of holotype 0.26 times that of length. All slopes nearly straight. Outline in dorsal view elongate-oval, anterior end slightly broader than posterior; sides of shell slightly raised relative to ends. Apex slightly anterior to center, at highest point of shell. Shell of most specimens with scattered, shallow eroded areas. Protoconch (Figure 6) lost in all but small specimens under 2 mm in length; protoconch posteriorly directed, length 170 μ m, sculpture of fine pits aligned in rows. Teleoconch

sculpture of fine concentric ridges, ridges sometimes coalescing; interspaces with aligned rows of pits (Figure 6); pits larger than those of protoconch, present at all stages of growth. Radial sculpture lacking. Shell margin sharp, easily chipped; interior transparent, showing exterior pattern of erosion; position of muscle scar not visible in shell interior.

Dimensions: Length 4.7, width 3.5, height 1.2 mm (holotype).

External anatomy (Figures 4, 5) as described for genus.

Radula (Figures 7, 8): Shaft of rachidian tooth broad, laterally constricted near base, upper edge with thick swelling, uncusped. First and second lateral fused at midshaft and having fused cusps. First lateral large, extending well above position of rachidian, its cusp with fine serrations on inner side and beaklike cusp at tip, which derives from second lateral. Fused second lateral with strong lateral projection. Third and fourth laterals with lateral curvature and long beaklike cusps. Fifth lateral reduced to shaft base only. Marginals numerous, with pointed cusps and serrations, similar in size.

Type locality: Along axis of East Pacific Rise near 12°N (11°51'N, 103°50'W), on wood, 2700 m.

Type material: 14 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2000, 22 March 1988. Holotype LACM 2434, 7 paratypes LACM 2435, 6 paratypes USNM 784764.

Remarks: Although only 2 of the 14 specimens retained the protoconch, the specimens of this species are otherwise in good condition, not showing the nearly complete erosion of the shell that is often characteristic of pseudococculinid as well as cocculinid species. The gill leaflets are so small that they can readily be seen only on one of the paratype specimens; unfortunately they are not apparent in Figure 5.

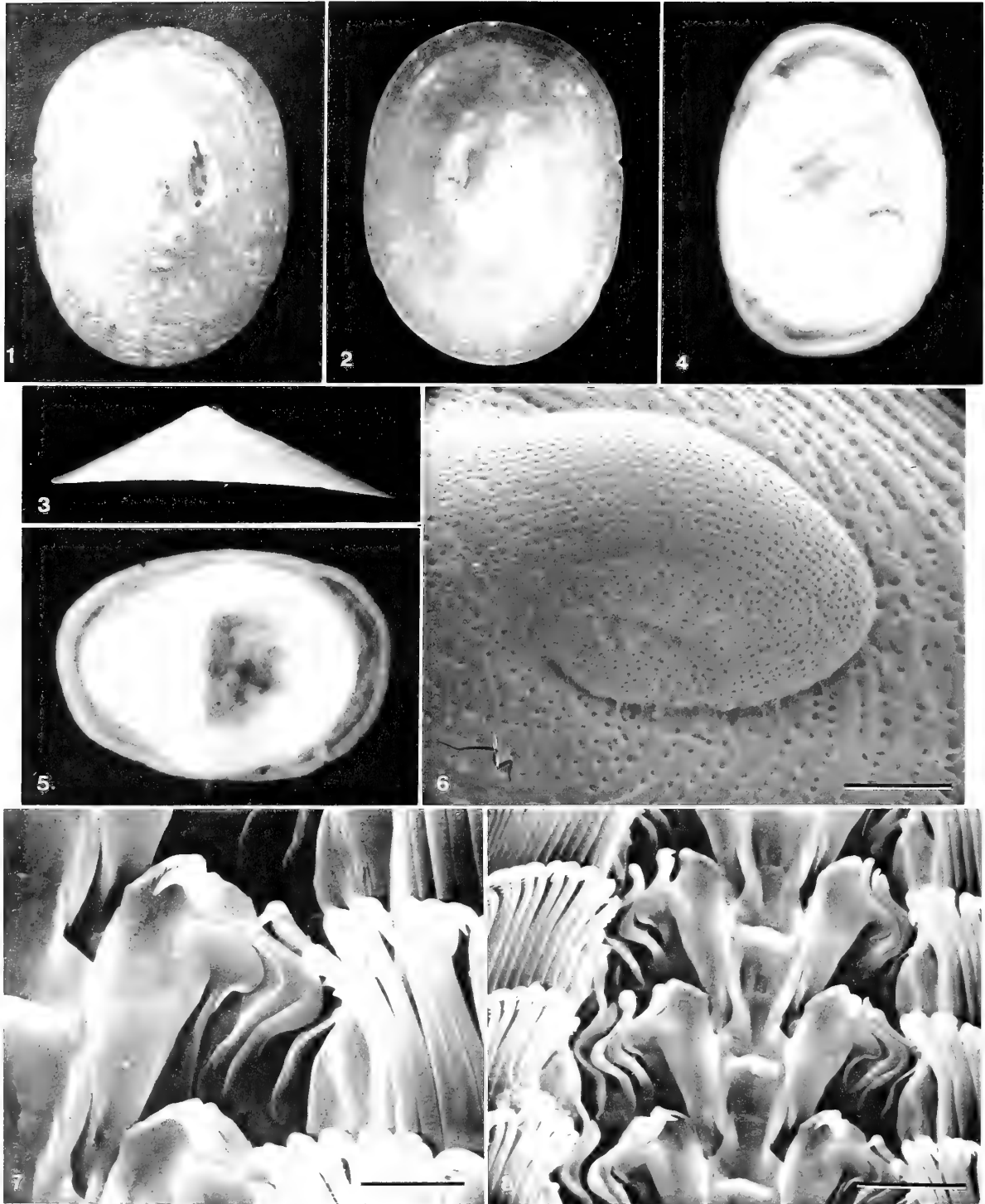
Etymology: The specific name honors Paul Tibbetts, one of the pilots of *Alvin*, marking *Alvin* dive 2000, a major peak in the history of undersea exploration.

Caymanabyssia Moskalev, 1976

Type species: *C. spina* Moskalev, 1976.

Diagnosis: Shell sculpture dominated by pustules superimposed on anastomosing network of surface sculpture; protoconch microsculpture of columnar crystals. Eyes lacking, oral lappets present, several gill leaflets present on right side; single leaflet on left; right cephalic tentacle of same size or slightly larger than left; epipodial tentacles a single posterior pair. Radula degenerate, rachidian and laterals lacking cusps.

Remarks: MARSHALL (1986) allowed a species in *Caymanabyssia* that lacked the conical granules that dominate the teleoconch sculpture of the type species of the genus. The discovery of another species with the same lack of a



Explanation of Figures 1 to 8

Figures 1–8. *Punctabyssia tibbetssi* McLean, sp. nov. *Alvin* dive 2000, near 12°N, 2700 m. Anterior at top in vertical views. Figures 1–3. Holotype, LACM 2434. Exterior, interior, and left lateral views. Length 4.7 mm. Figure 4. Dorsal view of holotype body, showing contracted right cephalic tentacle larger than left through mantle skirt. Length 3.0 mm. Figure 5. Ventral view of holotype body, showing posterior pair of epipodial tentacles at right; gill leaflets obscured by foot. Length 3.0 mm. Figure 6. SEM view of protoconch and early teleoconch, oblique view from left side, showing pits on protoconch and teleoconch. Scale bar = 40 μ m. Figure 7. SEM view of half-rows of radular ribbon. Scale bar = 10 μ m. Figure 8. SEM view of nearly full width of radular ribbon. Scale bar = 20 μ m.

major sculptural element warrants the separation of the two species at least at the subgeneric level. Accordingly the subgenus *Dictyabyssia* is described below.

Dictyabyssia McLean, subgen. nov.
(of *Caymanabyssia* Moskalev, 1976)

Type species: *Caymanabyssia sinespina* Marshall, 1986.

Diagnosis: Surface sculpture of anastomosing threads; lacking conical granules. Protoconch (where known) sculptured with minute columnar crystals. External anatomy and radula as in typical subgenus.

Remarks: The need for this subgenus is noted above. Marshall's species is selected as the type species of the new subgenus because it has an intact protoconch, which is missing on specimens of the species described here.

Two species are known in *Dictyabyssia*, the type species and the following new species.

Etymology: The name combines the Greek noun *dictyon*, meaning net, with reference to the anastomosing sculpture, plus the word-ending first used by MOSKALEV (1976) for genera related to *Pseudococculina*.

Caymanabyssia (Dictyabyssia) fosteri McLean,
sp. nov.

(Figures 9–16)

Description: Shell (Figures 9–11, 14, 15) of medium size for family (maximum length 5.7 mm), translucent white, periostracum very thin. Height moderate, that of holotype 0.46 times that of length. All slopes weakly concave. Outline in dorsal view elongate-oval, anterior narrower than posterior; margin of aperture nearly resting in same plane. Apex at $\frac{2}{3}$ shell length from anterior end, at highest point of shell. Protoconch unknown; apical area eroded in all specimens (none smaller than 2.5 mm). Teleoconch sculpture preserved at margin of smallest specimens, consisting of concentric growth irregularities and fine, densely anastomosing surficial threads (Figures 14, 15) visible under high magnification. Radial sculpture lacking. Entire surface of all specimens over 4 mm in length deeply eroded, showing coalescing linear pattern typical in family (Figure 9). Position of muscle scar marked by thick callus deposits in dorsal view (Figure 9), showing the inward expansion of scar characteristic of family. Shell margin sharp, easily chipped. Interior glossy white, outline of muscle scar well marked in mature specimens, anterior pallial attachment scar also marked. Shell interior thickened within to compensate for exterior erosion.

Dimensions: Length 5.7, width 4.2, height 2.6 mm (holotype).

External anatomy (Figures 12, 13) as defined for genus.

Radula (Figure 16): Rachidian tooth quadrangular, outer edges thickened, upper edge thin, uncusped. First lateral tooth elongate and tilted, cusp rows of laterals higher than

that of rachidian. First four laterals with projecting nubs but no overhanging cusps. Fifth lateral reduced to stubby basal portion. Marginal teeth of similar size, with long, beaklike cusps.

Type locality: Along axis of East Pacific Rise near 12°N (11°51'N, 103°50'W), on wood from 2700 m.

Type material: 19 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2000, 22 March 1988. Holotype LACM 2436, 10 paratypes LACM 2437, 8 paratypes USNM 784765.

Remarks: *Caymanabyssia (Dictyabyssia) fosteri* reaches a much larger size than *C. (D.) sinespina* Marshall, 1986, from New Zealand (5.8 mm, compared to 2.15 mm). In addition, the anastomosing sculpture of the immature specimen of *C. (D.) fosteri* (Figure 15) is much more dense than that illustrated by Marshall for *C. (D.) sinespina*.

Radulae of all species of *Caymanabyssia* s.s. and *C. (Dictyabyssia)* are similar, characterized by MARSHALL (1986) as "degenerate" in lacking cusps on the rachidian and laterals.

Etymology: The specific name honors Dudley Foster, senior pilot of the *Alvin*, on the occasion of the hallmark *Alvin* dive 2000.

Caymanabyssia (Caymanabyssia) vandoverae McLean,
sp. nov.

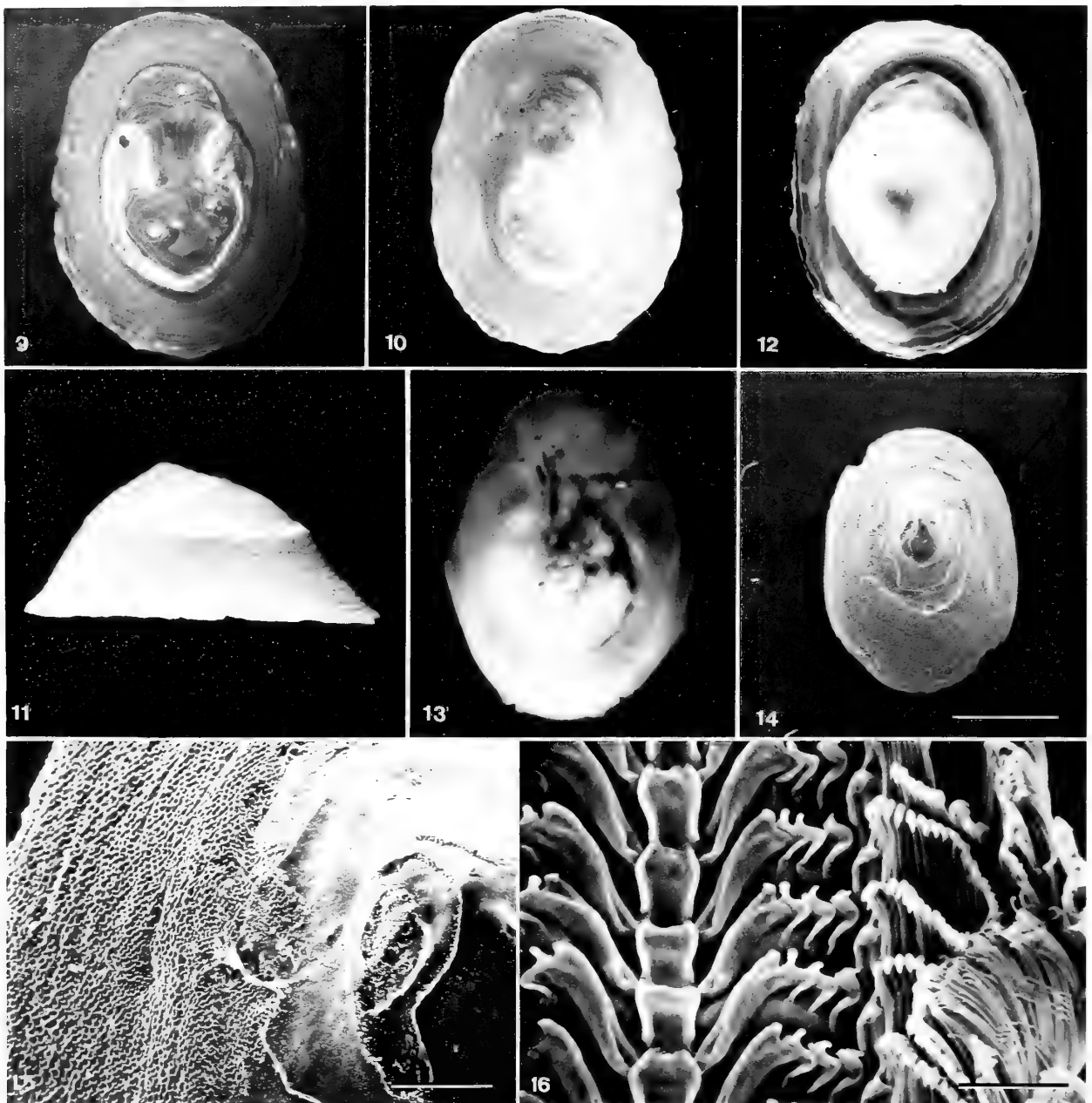
(Figures 17–24)

Description: Shell (Figures 17, 18, 22–24) of small size for family but typical size for genus (maximum length 3.9 mm), translucent white, periostracum very thin. Height low, that of holotype 0.25 times that of length. All slopes slightly convex. Outline in dorsal view elongate-oval, anterior end same width as posterior; sides of shell raised relative to ends. Apex nearly central, at highest point of shell. Protoconch (Figures 22–24) posteriorly directed, length 200 μ m, sculpture of clumped columnar prisms, usually lost in specimens over 3.0 mm in length. Teleoconch sculpture of prominent pustules aligned in curving rows, superimposed on microsculpture of finely anastomosing threads; threads visible only under high magnification. Radial sculpture lacking. Sculpture preserved in large specimens, although scattered erosional pits are present. Interior surface translucent white, revealing position of exterior erosional pits and only faintly indicating position of muscle scar. Shell edge showing position of exterior pustules.

Dimensions: Length 3.6, width 2.7, height 0.9 mm (holotype).

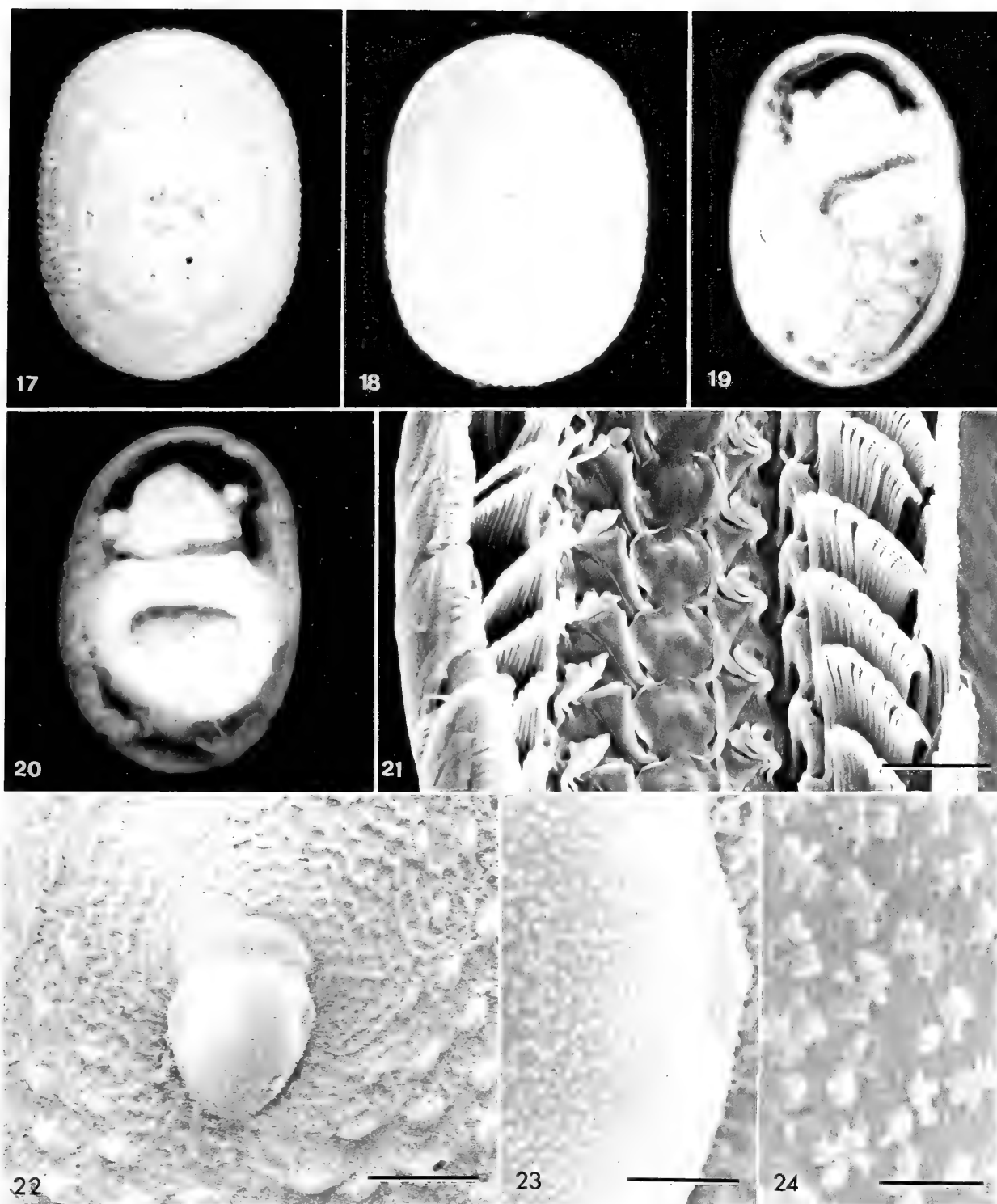
External anatomy (Figures 19, 20) as defined for genus.

Radula (Figure 21): Rachidian plate broad, thin, raised at edges, lacking overhanging cusp. First lateral tooth extending to height of rachidian, with strong lateral projection, lacking cusp. Second, third, and fourth laterals with



Explanation of Figures 9 to 16

Figures 9–16. *Caymanabyssia* (*Dictyabyssia*) *fosteri* McLean, sp. nov. *Alvin* dive 2000, near 12°N, 2700 m. Anterior at top in vertical views. Figures 9–11. Holotype, LACM 2436. Exterior, interior, and left lateral views (surface sculpture eroded). Length 5.7 mm. Figure 12. Ventral view of paratype body attached to shell, showing paired posterior epipodial tentacles. Length 5.6 mm. Figure 13. Dorsal view of same specimen detached from shell, showing cephalic tentacles of nearly equal size. Length 3.0 mm. Figure 14. SEM view of juvenile shell with intact surface sculpture, but eroded protoconch. Scale bar = 1 mm. Figure 15. SEM view of surface detail of anastomosing lines in same specimen as in Figure 14, eroded apical area at right. Scale bar = 200 μ m. Figure 16. SEM view of radular ribbon. Scale bar = 40 μ m.



Explanation of Figures 17 to 24

Figures 17–24. *Caymanabyssia* (*Caymanabyssia*) *vandoverae* McLean, sp. nov. *Alvin* dive 2034, Gorda Ridge, 3362 m. Anterior at top in vertical views. Figures 17, 18. Holotype, LACM 2438. Exterior and interior views. Length 3.9 mm. Figures 19, 20. Dorsal and ventral views of detached body of holotype, showing right cephalic tentacle slightly larger than left. Length 2.2 mm. Figure 21. SEM view of radular ribbon. Scale bar = 40 μ m. Figure 22. SEM view of protoconch and teleoconch surface, showing pustules and anastomosing sculpture of teleoconch. Scale bar = 100 μ m. Figure 23. Detail of protoconch sculpture, showing columnar prisms. Scale bar = 60 μ m. Figure 24. Enlargement of columnar prisms in area outlined by rectangle of Figure 23. Scale bar = 15 μ m.

lateral elbows, lacking cusps. Fifth lateral elongate, with two basal prongs to shaft, cusps lacking. Marginal teeth numerous, long and slender, with sharp cusp and serrations, nearly equal in size.

Type locality: Escanaba Trough, Gorda Ridge (41°00.4'N, 127°29.3'W), on wood, 3362 m.

Type material: 5 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2034, 4 June 1988. Holotype LACM 2438, 4 paratypes LACM 2439, 1 paratype USNM 784766.

Remarks: *Caymanabyssia vandoverae* is clearly a member of subgenus *Caymanabyssia* in having the sculpture dominated by pustules superimposed on an anastomosing network of surface sculpture, having the protoconch microsculpture of columnar crystals, and having a radula lacking cusps on the rachidian and laterals. The dorsal sperm groove is prominent and may be seen by probing the tentacle in ventral view. The new species is the third member of the genus. Other species are the type species from the Cayman Trough in the Western Atlantic, and *C. rhina* Marshall, 1986, from off White Island, New Zealand. It differs from *C. rhina* in having much more prominent and densely spaced pustules. Moskalev's *C. spina* also has more broadly spaced pustules than *C. vandoverae*.

Etymology: The name honors Dr. Cindy Van Dover, of Woods Hole Oceanographic Institution, who is responsible for the preservation and forwarding of each species described herein.

Amphiplica Haszprunar, 1988

Type species: *A. venezuelensis* McLean, 1988.

Diagnosis: Shell size large for family; white, periostracum thin; protoconch unknown; teleoconch sculpture of sharply raised concentric ridges. Eyes lacking, right tentacle similar in size to left; up to six pairs of secondary subpallial gill leaflets on both sides near anterior end of foot; oral lappets present; epipodial tentacles a single posterior pair. Rachidian tooth prominent, tapered, with beaklike cusp; lateral teeth with sharply pointed cusps; fifth lateral with five short denticles; innermost marginals larger than the rest.

Remarks: The new species described below has the sharply raised concentric sculpture, the secondary gill lamellae on both sides, and the oral lappets (although more weakly developed) of *Amphiplica*, but differs in its smaller size, having a more posterior apex, retaining the protoconch in mature sizes, and radular differences (four strong rather than five weak cusps on the fifth lateral, the second marginal tooth not larger than the others). The three members of *Amphiplica* s.s. (*A. venezuelensis* McLean, 1988, *A. knudseni* McLean, 1988, and *A. concentrica* (Thiele, 1909)) are the largest known members of the family. These three species lose the protoconch at an early age.

These differences are recognized at the subgeneric level.

***Gordabyssia* McLean, subgen. nov.**
(of *Amphiplica* Haszprunar, 1988)

Type species: *Amphiplica* (*Gordabyssia*) *gordensis* McLean, sp. nov.

Diagnosis: Shell small, white, periostracum thin; protoconch with subreticulate pattern of anastomosing threads in longitudinal rows; teleoconch sculpture of sharply raised concentric ridges. Eyes lacking, right tentacle similar in size to left; up to six pairs of secondary subpallial gill leaflets on both sides near anterior end of foot; epipodial tentacles a single posterior pair. Rachidian tooth prominent, tapered, cusp beaklike; lateral teeth with sharply pointed cusps; fifth lateral with four pointed cusps; innermost marginals larger than the rest.

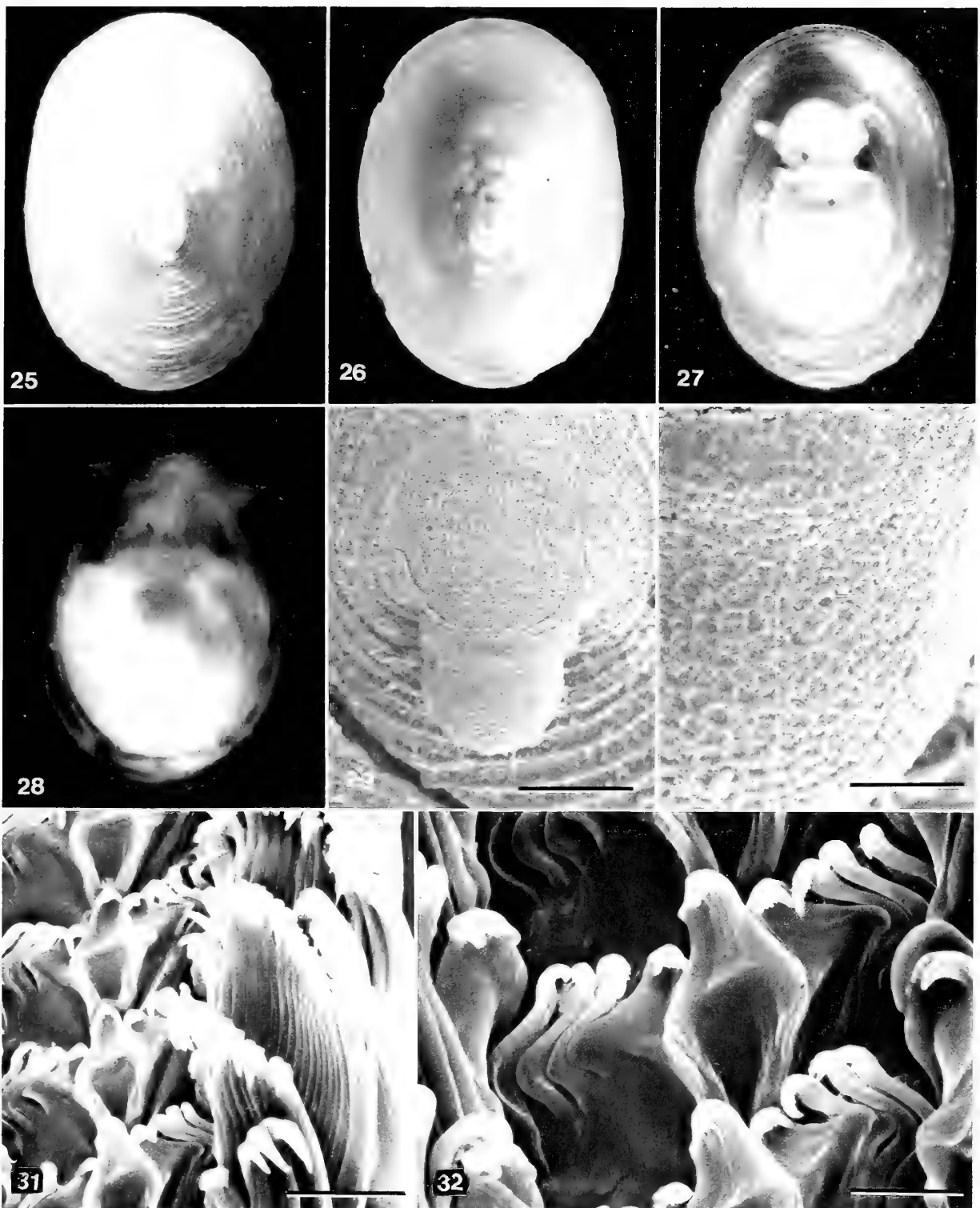
Remarks: Reasons to justify the new subgenus are given above. The new species described here provides a provisional protoconch definition for the genus *Amphiplica* s.s., as the protoconch is unknown in the typical subgenus. Should the protoconch in the typical subgenus prove to be of a different type, the subgenus *Gordabyssia* should be raised to a full genus. Similar protoconch sculpture to that of *Amphiplica* (*Gordabyssia*) *gordensis* is known in *Mesopelex* Marshall, 1986, and *Kurilabyssia* Moskalev, 1976, but characters of radula and teleoconch sculpture do not agree.

The new species is the only member of the family to be associated with sulfide crust at hydrothermal vents, albeit having a very limited distribution in the habitat. Specimens were collected from four stations in the Escanaba Trough on the Gorda Ridge, in each case on hard substrates, indicated as sulfide crust on the labels, so it is clear that this is not an association with wood, as in most other pseudococculinids. There seem to be no modifications that correlate with the hydrothermal-vent environment.

Amphiplica (*Gordabyssia*) *gordensis* McLean,
sp. nov.

(Figures 25–32)

Description: Shell (Figures 25–27, 29, 30) of medium size for family (maximum length 3.9 mm), translucent; periostracum thin, light brown. Height low, that of holotype 0.28 times that of length. Anterior and lateral slopes convex; posterior slope straight. Outline in dorsal view elongate-oval, anterior end about the same width; shell margin in same plane (sides or ends not raised). Apex posterior to center, at highest point of shell. Shell of most specimens with scattered, shallow eroded areas. Protoconch (Figures 29, 30) retained on most specimens, even on specimens with eroded apical area; protoconch posteriorly directed, length 200 μ m, sculpture of subreticulate pattern of anastomosing threads in longitudinal rows. Teleoconch sculp-



Explanation of Figures 25 to 32

Figures 25–32. *Amphipecta* (*Gordabyssia*) *gordensis* McLean, sp. nov. *Alvin* dive 2035, Gorda Ridge, 3305 m. Anterior at top in vertical views. Figures 25, 26. Holotype, LACM 2440. Exterior and interior views. Length 3.9 mm. Figure 27. Ventral view of holotype body attached to shell, showing paired gill leaflets near both sides of foot. Length 3.9 mm. Figure 28. Dorsal view of detached body of holotype. Length 2.1 mm. Figure 29. SEM view of protoconch (with subreticulate sculpture) and teloconch surface (concentric sculpture). Scale bar = 100 μ m. Figure 30. Enlarged view of subreticulate sculpture of protoconch. Scale bar = 25 μ m. Figure 31. SEM view of radular ribbon. Scale bar = 25 μ m. Figure 32. Enlarged view of central field, showing four cusps on fifth lateral tooth. Scale bar = 12 μ m.

ture of fine, sharp concentric ridges, ridges not coalescing. Radial sculpture of exceedingly fine striae, detectable under high magnification, producing fine swellings on crossing concentric ridges. Shell margin sharp, easily chipped; interior transparent, showing exterior pattern of erosion; position of muscle scar faintly visible in shell interior.

Dimensions: Length 3.9 mm, width 2.8 mm, height 1.1 mm (holotype).

External anatomy (Figures 27, 28) as described for genus and subgenus.

Radula (Figures 31, 32): Rachidian tooth elongate, rising above level of all lateral teeth, having simple beaklike overhanging cusp, central part of shaft laterally expanded. First pair of laterals with strong lateral projection, overhanging cusp with long tip and serrations on inner side; second, third, and fourth laterals similarly shaped, cusps with single pointed tip and serrations on both sides. Fifth lateral tooth massive, with four pointed cusps; marginal teeth with long overhanging cusps, the second, third, fourth and fifth pairs having the longest cusps.

Type locality: Escanaba Trough, Gorda Ridge (41°00.4'N, 127°29.3'W), on sulfide crust, 3305 m.

Type material: 34 specimens from type locality, collected with deep-submersible *Alvin*, dive No. 2035, 5 June 1988. Holotype LACM 2440, 18 paratypes LACM 2441, 15 paratypes USNM 784767.

Additional paratypes were taken at four other *Alvin* dives at the type locality (same coordinates for each dive but different depths and dates): LACM 2441a, 5 specimens, dive 2033, 3356 m, 3 June 1988; LACM 2441b, 4 specimens, dive 2039, 3305 m, 9 June 1988; LACM 2441c, 9 specimens, dive 2040, 3271 m, 10 June 1988; LACM 2441d, 1 specimen, dive 2042, 3271 m, 12 June 1988.

Remarks: This species exhibits considerable variation in shell proportions and in the degree of erosion. A number of specimens were smaller, more elevated and with more compressed sides than the holotype. Most specimens retain the protoconch, even though the surface sculpture on the anterior slope may be eroded.

One other limpet has recently been described from the Escanaba Trough on the Gorda Ridge: *Neoleptopsis gordensis* McLean, 1990. A general report on the hydrothermal-vent fauna of the Escanaba Trough on the Gorda Ridge is given by VAN DOVER *et al.* (1990).

Etymology: The specific name derives from the type locality, the Gorda Ridge.

DISCUSSION

Until now the family Pseudococculinidae has been represented in the Eastern Pacific by a single species, *Yaqinabyssia careyi* McLean, 1988, from the Cascadia Abyssal Plain off Oregon. The four species described here bring the total to five species for the family in the Eastern Pacific.

The use of a deep-submersible research submarine has provided new opportunities to locate and sample "islands" of biogenic origin, a sparse habitat in the deep sea (TURNER, 1978). Further opportunities should be taken whenever possible to sample additional wood falls on dives made by deep-submersibles. The sparsity of records indicates that our knowledge of distribution is minimal and that additional species of Pseudococculinidae may remain to be discovered.

New limits to character states in the family Pseudococculinidae are provided here by the new monotypic genus *Punctabyssia*, which has a unique protoconch with pits aligned in rows and radular tooth elements that show a derived state of fusion between the first and second lateral tooth elements, which in all other genera are separate elements.

The new subgenus *Dictyabyssia* (of *Caymanabyssia*) flags the existence of two species that lack the most prominent sculptural element of typical *Caymanabyssia*.

The new subgenus *Gordabyssia* (of *Amphiplica*) provides an exception to the rule that pseudococculinids are always associated with biogenic substrates. One other cocculiniform family, the Pyropeltidae, described by McLEAN & HASZPRUNAR (1987) occurs in the hydrothermal-vent habitat.

MARSHALL (1986) defined a number of pseudococculinid genera on characters of the radula, protoconch, and external anatomy; HASZPRUNAR (1988a) added anatomical definitions, recognizing a total of 11 genera. Two subfamilies were originally defined by MARSHALL (1986), the Pseudococculinae and Caymanabyssinae, in large part on radular characters. Diagnoses were altered by HASZPRUNAR (1988a:175–176), who questioned the validity of radular characters as a basis for subfamily distinctions and based his own definitions on gill and protoconch characters. However, the utility of a two-fold subdivision is questioned here because the new species *Amphiplica* (*Gordabyssia*) *gordensis* has gill characters of Caymanabyssinae and protoconch characters more typical of Pseudococculinae. Accordingly, a subfamily division is not recognized here. Until more is known about how characters combine in this family it may be premature to arrive at a robust classification.

ACKNOWLEDGMENTS

I am especially grateful to Dr. Cindy Van Dover of Woods Hole Oceanographic Institution, who was aboard the expeditions of the *Alvin* when the specimens were collected, for preserving the specimens of each of the four species and forwarding them to me. She has also read the manuscript and provided helpful comments. I thank Clif Coney for operating the scanning electron microscope at the Center for Electron Microscopy and Microanalysis, University of Southern California, and Bertram C. Draper for the photos of preserved animals. I thank reviewers Carole S.

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A New Species of *Flabellina* (Nudibranchia: Aeolidacea) from Oshoro Bay, Japan

by

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Abstract. *Flabellina amabilis* sp. nov. from Oshoro Bay, western Hokkaido, Japan, is described and illustrated. The living animal can be distinguished easily from closely related species by the particular patterns of white coloration on the body, the morphology of the foot corners, the ceratal arrangement, the position of the anus and gonopore, and the unique shape of its penis.

INTRODUCTION

During the course of an ecological survey on *Flabellina athadona* (Bergh, 1875) at Oshoro Bay (Sea of Japan), western Hokkaido (see map, HIRANO & HIRANO, 1985), a new and closely related species also belonging to the Flabellinidae was found during the same season. This paper describes the external and internal morphology of this new species and compares it with closely allied congeners. All descriptions are based upon living animals because the discrimination between this species and *F. athadona* is especially difficult after preservation. Although we have examined hundreds of specimens, only specimens selected for the type series are described and figured.

DESCRIPTION

Flabellina amabilis Hirano & Kuzirian, sp. nov.

(Figures 1-7)

Type material: Holotype, National Science Museum of Tokyo (catalogue number NSMT-MO66330), specimen collected 26 February 1985, Oshoro Bay, Hokkaido, Japan. Ten paratypes, NSMT-MO66331, from the same sample; color transparencies also on file.

Distribution and habitat: Despite the fact that various localities in Hokkaido and Honshu, mainland Japan, have been sampled, this species has been found only at Oshoro Bay, western Hokkaido. Specimens were found on athecate hydroid colonies of *Eudendrium boreale* Yamada, 1954, attached to intertidal or subtidal rocky substrates.

Etymology: This species is named for its charming appearance and countenance when seen alive and in its natural habitat. The Japanese name "Pirika-minoumushi" is assigned: "pirika" means pretty or beautiful in the Ainu (the language of Ainu) and "minoumushi" means aeolid nudibranch in Japanese.

External morphology: Body translucent white, with pale orange or salmon pink viscera. Diverticula of digestive gland within cerata reddish orange, carmine, or sometimes tan to dark brown. Opaque white specks on dorsal surfaces of tips of oral tentacles, and entire distal half of rhinophores; basally, white coloration only on dorsal surface of rhinophores. Cerata with opaque white dots or flecks occurring sparsely around distal half of ceratal surfaces, seldom found on lower half. Similar opaque white flecks restricted to central line on dorsal tail surface; not found on any other dorsal body surface (Figures 1, 2A).

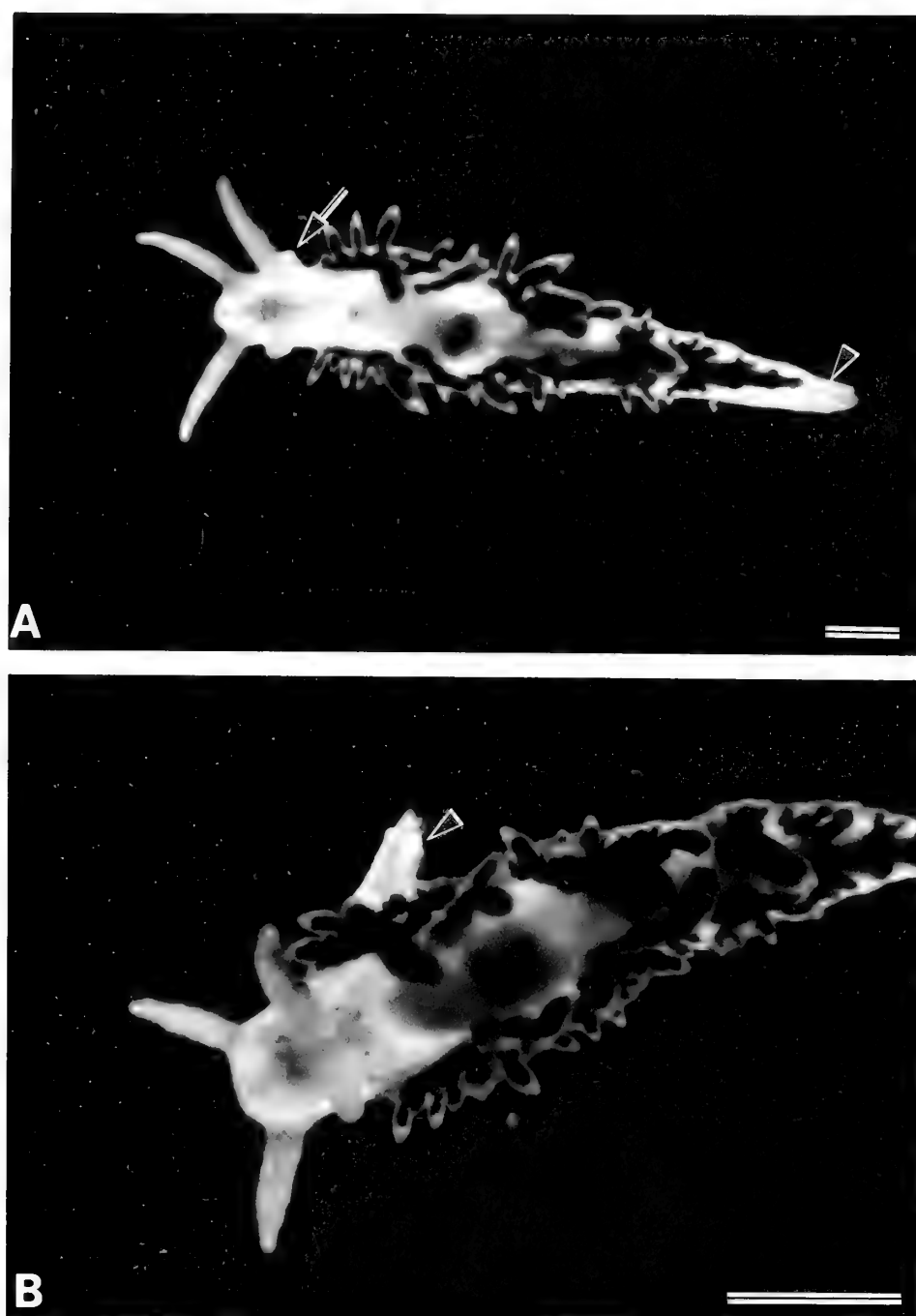


Figure 1

Flabellina amabilis Hirano & Kuzirian, sp. nov. A. Dorsal view of live animal, illustrating short, pointed anterior foot corners (arrow) and opaque white stripe occurring on tail only (arrowhead). B. Dorsal view of another animal with its long, conical penis everted (scales = 3.0 mm).

Extended body length to 26 mm. Body long, high, but not very narrow in comparison of width-to-length proportions. Notal brim prominent and continuous; pericardium situated between one-half and one-third of body

length from anterior end; tail approximately one-fifth to one-seventh of body length.

Foot equaling width of visceral portion of body, lateral margin flared, undulate, extending with long gentle taper

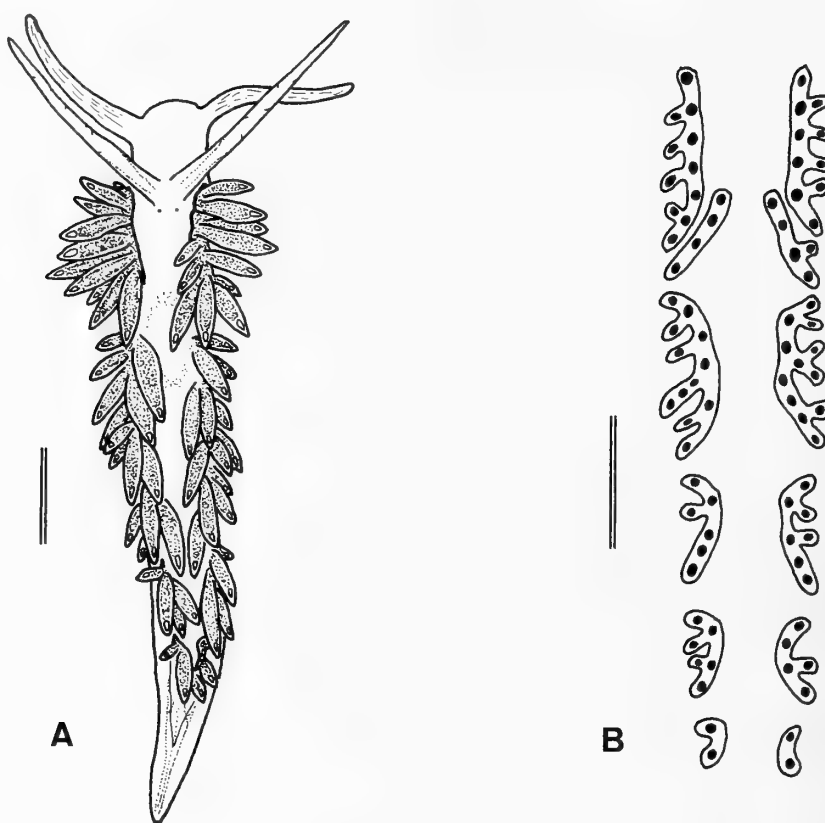


Figure 2

Flabellina amabilis. A. Diagrammatic illustration of 15-mm-long animal, depicting general body form, ceratal arrangement, and patterns of opaque white body coloration on oral tentacles, rhinophores, and tail. B. Schematic diagram of ceratal clusters and branching patterns (scales = 2.0 mm).

to pointed tail; anterior foot margin with transverse labial groove, slightly notched medially; anterior foot corners only slightly pointed, not tentaculiform and difficult to distinguish in preserved material (Figure 3).

Oral tentacles about one-fifth to one-sixth of body length, tapering gradually to rounded tip. Rhinophores slightly longer and narrower than oral tentacles, moderately tapered to bluntly tipped. Oral tentacles with smooth surface; rhinophores slightly verrucose.

Cerata arranged in five to six clusters; most posterior cluster difficult to distinguish bilaterally. First and second cluster with five to six loosely defined rows, remainder with three to four rows (Figure 2B); lateral cerata lining notal brim very small, medial ones longest. Each fully developed ceras fusiform, lanceolate to linear in outline; cnidosac prominent, ovoid or conical.

Interhepatic space small. Anus pleuroproct, lying below third or fourth ceratal row of second cluster, just ventral to notum. Renal pore clearly visible and situated within 1 mm anterior to anus and slightly more dorsal. Gonopore located beneath anterior to middle of first ceratal cluster (Figure 3).

Buccal cavity: Jaws ovoid with prominent masticatory border bearing 5 or 6 rows of distinct denticles (Figure 4). Oral glands absent; pair of typical, elongate salivary glands present with ducts passing through circumoesophageal nervous system and entering buccal mass on each side of oesophagus. Radula triseriate, formula equals $13-17 \times 1 \cdot 1 \cdot 1$. Rachidian tooth with 5-7 denticles bilaterally, denticles slightly curved toward large central cusp. Lateral teeth sickle-shaped with 6-8 denticles on inner side (Figure 5).

Reproductive system: System androdiaulic (Figures 6, 7; especially see Figure 7 for a functional description of the reproductive system). Gonad large, pale orange to salmon pink; follicles tightly packed with moderately small, female acini peripherally. Pre-ampullary duct runs centrally within gonad, along right side of main posterior ceratal duct; duct expands into ampulla of only one loop from which emerges narrow post-ampullary duct, lying below bursa and within folds of mucous gland. Distally, duct divides into oviduct and prostatic vas deferens. Proximal oviduct loops posteriorly and expands into large bulbous

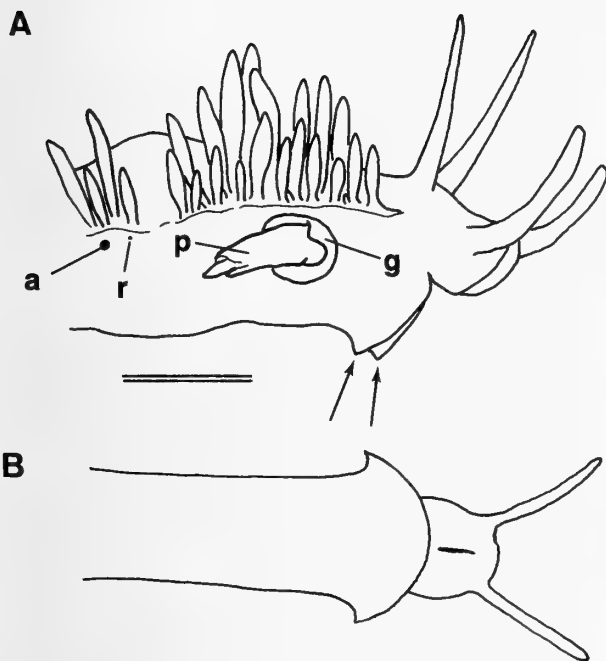


Figure 3

Flabellina amabilis. A. Sketch of animal's anterior right side illustrating positions of anus (a), renopore (r), common gonopore (g) with everted conical penis (p), and short, pointed anterior foot corners (arrows) (scale = 2.0 mm). B. Ventral view of the animal.

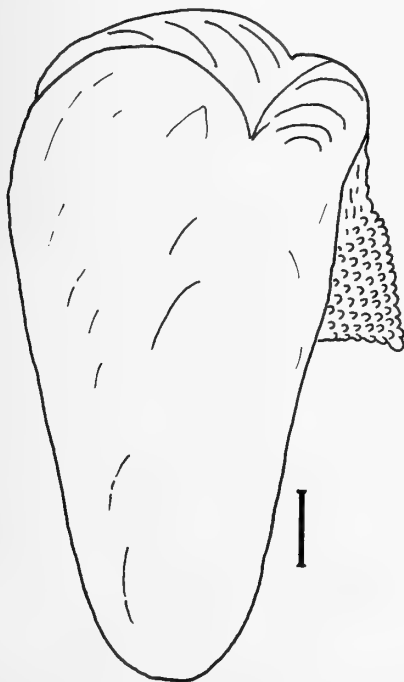


Figure 4

Flabellina amabilis. Diagram of single jaw plate with denticulate masticatory border (scale = 120 μ m).

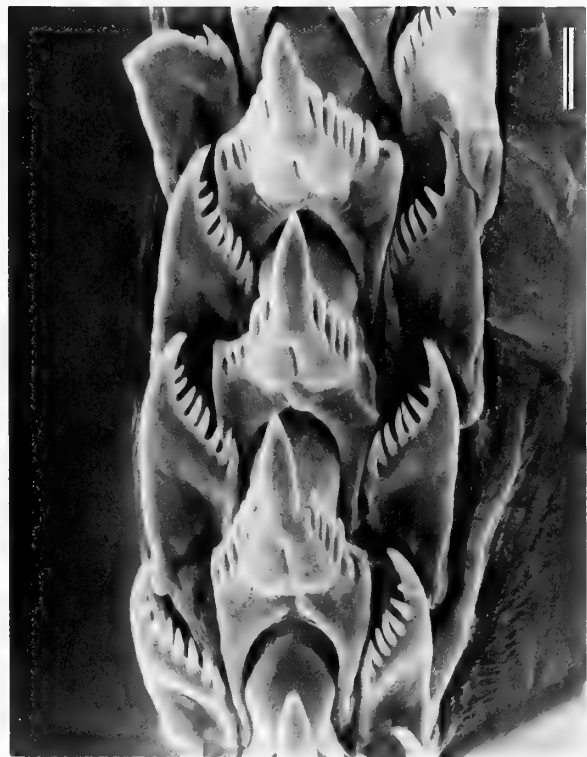


Figure 5

Flabellina amabilis. Scanning electron microscopical image of three complete radular teeth rows, illustrating central rachidian and lateral (2) tooth morphology (scale = 20 μ m).

serial receptaculum seminis, which continues anteriorly as distal oviduct and enters albumen gland. Prostatic vas deferens long, smooth, muscular, consisting of 4 or 5 tightly coiled loops; distally tapers into small preputium. Penis long, thin, unarmed with sharply pointed tip surrounded by thin membranous sheath (Figure 1B). Nidamental and penial apertures contained in common external gonopore. Bursa copulatrix bulbous with long narrow duct inserting dorsally into nidamental duct, just internal to gonopore.

Reproductive cycle: Spawning with large numbers of egg masses has been observed yearly during the winter season (late December–early April) at Oshoro Bay from 1983 to 1988. The egg mass consists of a thin undulate coil (type B; HURST, 1967) containing singly encapsulated eggs measuring 60–65 μ m in diameter. The capsule itself is oval and measures 90–100 μ m long by 70–85 μ m wide. Embryos develop into planktotrophic veligers with spiralled, type I shells (THOMPSON, 1961).

DISCUSSION

GOSLINER & GRIFFITHS (1981) regarded *Coryphella* Gray, 1850, as a junior subjective synonym of *Flabellina* Voigt, 1834, on the basis of priority, after comparing the simi-

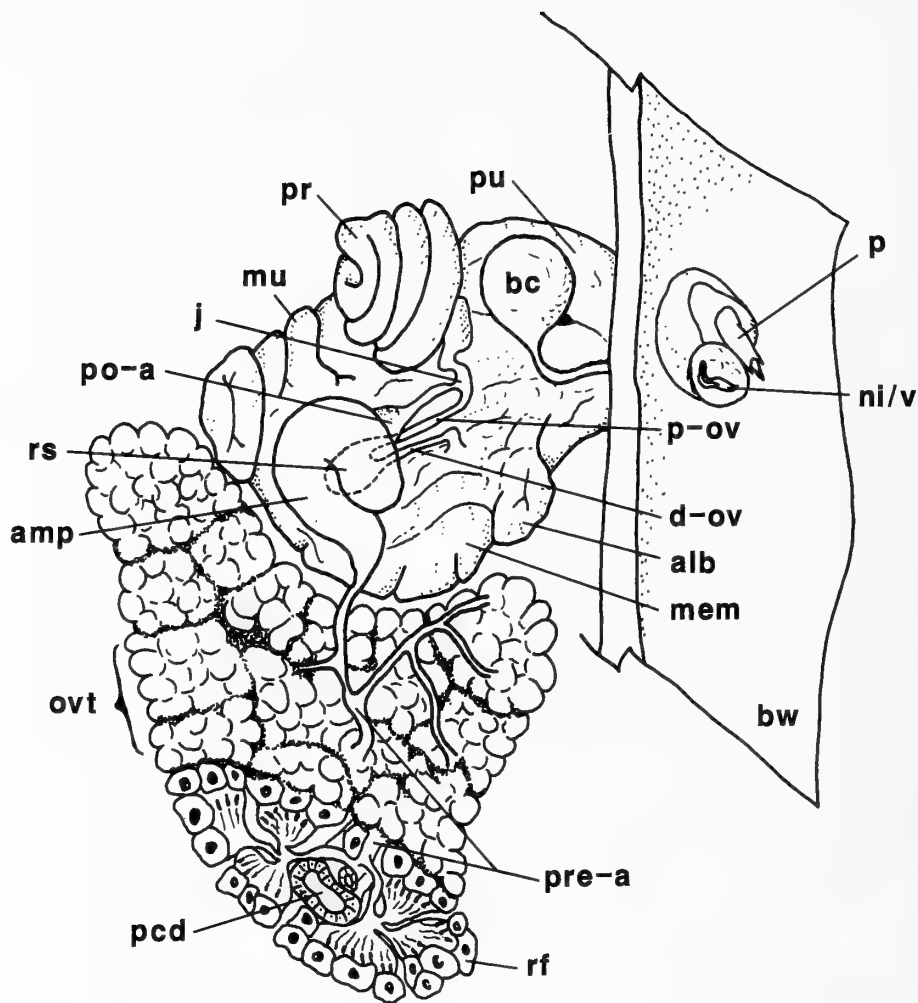


Figure 6

Flabellina amabilis. Diagram of reproductive system depicting configuration and placement of major components: alb, albumen gland; amp, ampulla; bc, bursa copulatrix; bw, portion of external body wall; d-ov, distal oviduct; j, junctional separation of male and female pallial gonoducts; mem, membrane gland; mu, mucous gland; ni/v, nidamental/vaginal opening; ovt, ovotestis; p, conical penis; pcd, posterior ceratal duct; po-a, post-ampullary duct; p-ov, proximal oviduct; pr, prostatic vas deferens; pre-a, pre-ampullary duct; pu, preputium; rf, cross-section of reproductive follicle illustrating peripherally developing oocytes, medially developing sperm, and small basal ductule emptying each follicle into pre-ampullary duct; rs, receptaculum seminis.

larities and differences between the two genera. The taxon *Flabellina*, as it now stands, comprises a widely divergent and ponderous assemblage of species, especially when one considers the extremes in plesiomorphic and derived characters. However, if the taxon is analyzed by species, there is a continuum of overlapping character states throughout. Therefore, we have tentatively accepted this taxonomic change, but realize that the synonymy has not gained universal acceptance.

Flabellina amabilis sp. nov. can be distinguished from its congeners reported from the Sea of Japan and Pacific coasts of Japan on the basis of numerous morphologic

characters (Table 1). When compared with living specimens of *F. abei* (BABA, 1987a), *F. amabilis* can be identified by the presence of an opaque white line on the tail only and dorsal surfaces of the tips of the oral tentacles. The head of *F. abei* has a bold, opaque-white letter "Y" in the center, while the oral tentacles bear a white line along the posterior surface. *Flabellina abei* also possesses a common genital atrium with the gonopore located on the right side below the center of the first ceratal cluster, and the anus is located at the posterior edge of the interhepatic space below the first row of cerata of the second cluster. In contrast, *F. amabilis* has no genital atrium and the com-

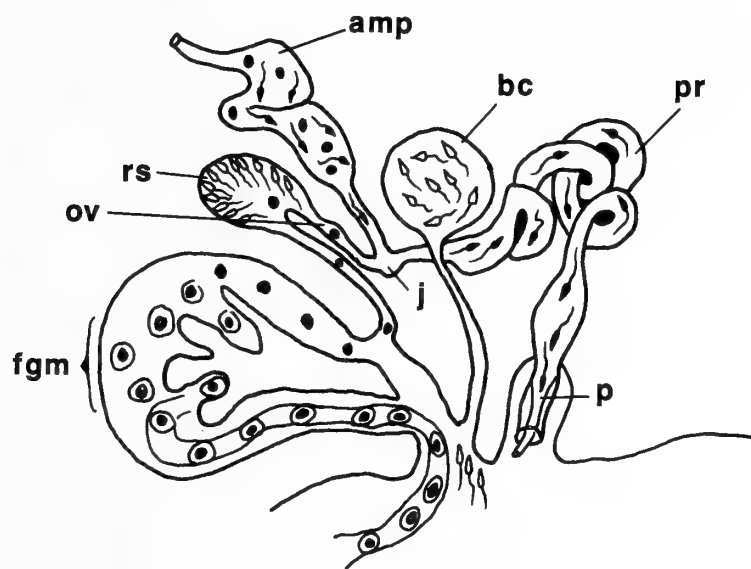


Figure 7

Flabellina amabilis. Schematic representation of distal gland mass of reproductive system, depicting major components with their function: endogenous sperm (solid sperm heads) and oocytes (solid circles) in arrested metaphase traverse the ampulla (amp) to junction (j) where male and female pallial gonoducts separate; oocytes travel through oviduct (ov), receptaculum seminis (rs) where exogenous sperm (open sperm heads) are stored embedded within lining epithelium and fertilization putatively occurs, then into female gland mass (fgm) where eggs are encapsulated and collated into egg ribbon before exiting via nidamental opening; endogenous sperm travel through prostatic vas deferens (pr) and during copulation are deposited by penis (p) into female vaginal opening (common with nidamental opening in this species); these now exogenous sperm are initially received in bursa copulatrix (bc) which dissolves prostatic secretions, thus allowing sperm to move into receptaculum seminis (rs) for nourishment and storage.

Table 1
Morphologic characters of major Japanese species of *Flabellina*.

Character state	<i>F. amabilis</i>	<i>F. abei</i>	<i>F. athadona</i>
White coloration			
Body	tail stripe only	head only; letter "Y"	Y-shaped, dorsal stripe; tip oral tentacles to tail
Oral tentacles	speckled	stripe; posterior edge	stripe; as above
Cerata	speckled tips	speckled, white tips	speckled
Ceratal arrangement	5-6 clusters; 3-6 rows/cluster	5 clusters	6 clusters; 5-6 rows/cluster
Notum	distinct	distinct	distinct; less interhepatic space
Foot corners	small, pointed	long, tentacular	rounded
Anal position, 2nd ceratal cluster	row 3-4	row 1	row 3
Gonopore, 1st ceratal cluster	anterior half	center	anterior half
Genital atrium (common)	absent	present	present; vestibular glands
Penis	conical	conical	"false"†
Radular formula	13-17 × 1.1.1	15 × 1.1.1	19-22 × 1.1.1
Denticulation			
Rachidian teeth	6-9	6-9	4-5
Lateral teeth	6-8	11-12	8-9
Central cusp of rachidian	long, wide	long, thin	short, wide

† BABA (1987b).

mon gonopore bearing the separate penial and nidamental openings is located beneath the anterior half of the first ceratal cluster. The color pattern of the other closely related species, *F. athadona* (Bergh, 1875), which has been described from living animals (BABA, 1987b), consists of a Y-shaped mid-dorsal white stripe extending from the tips of the oral tentacles to the tail. The gonopore of *F. athadona*, as diagrammed by BABA (1987b), serves as the opening for a common genital atrium and is located below the anterior half of the anterior right ceratal cluster. The anus of this species and of *F. amabilis* is similarly located beneath the third row of cerata of the second cluster. All three species can also be distinguished from each other using the morphology of the anterior foot corner. *Flabellina abei* has long, tentacular foot corners, while in *F. amabilis* they are only slightly pointed; *F. athadona* has rounded foot corners, resembling the condition generally found in most Eubranchidae and Tergipedidae.

The radular morphology of each species is also specific. *Flabellina abei* and *F. amabilis* have similar numbers of rows of teeth (15 vs. 13–17, respectively), but the two species differ markedly in rachidian tooth morphology, especially in the central cusp; the cusp is long and thin in *F. abei* and long and wide in *F. amabilis*. The lateral teeth of *F. abei* have many more medial denticles, although the basic sickle shape is similar in both. The character of 19–22 teeth rows in *F. athadona* is different from the previous two species, as is the rachidian tooth morphology and the smaller number of lateral denticles (4 or 5 only).

The specific differences between the three congeners also extend to the reproductive systems. *Flabellina athadona* differs in the shape of the penis, which consists of a folded and rolled extension of the preputial lining (false penis; BABA, 1987b) and also possesses a vestibular or preputial gland located at the posterior end of the preputium (personal observation; BABA, 1987b). *Flabellina abei* possesses a short conical penis distal to a short thick prostatic vas deferens and a common genital atrium or vestibule. The penis is also conical in *F. amabilis*, but the vas deferens is considerably longer than that which BABA (1987a) figured for *F. abei*. *Flabellina amabilis* also has separate male and female gonoporal openings contained in a common gonopore. All three species possess a saccular bursa copulatrix with a long narrow duct, but the insertion points into the nidamental duct differ among the species. The receptaculum seminis of *F. athadona* is semi-serial, while it is completely serial in *F. amabilis*. BABA (1987b) did not describe or figure either the oviduct or receptaculum for *F. abei*.

Of the other flabellinids known from the Sea of Japan, *Flabellina amabilis* differs from *F. orientalis* (Volodchenko, 1941) on the basis of radular morphology (the number of teeth rows, and the shape and denticulation pattern of rachidian and lateral teeth), the shape of the rhinophores, the foot, and the possession of nonclustered cerata. *Flabellina amabilis* can be distinguished from *F. verrucosa*

(Sars, 1829) reported from the Sea of Japan (VOLODCHENKO, 1955), on the basis of radular and penial morphology, as well as body coloration. *Flabellina alderi* (Adams, 1861), described from specimens collected off Matsumae, Hokkaido (Strait of Tsugaru), was cited by BERGH (1885) and listed by MARCUS (1961) as an uncertain species. Based on the cursory Latin description given by ADAMS (1861) of the general body shape and coloration, there are similarities between *F. alderi* and *F. amabilis*. However, the two appear to differ in the morphology and coloration of the oral tentacles and rhinophores.

When compared with the other described flabellinid species, *Flabellina amabilis* most closely resembles *F. gracilis* (Alder & Hancock, 1844). The general body morphology and ornamentation, with the opaque white stripes on the oral tentacles, rhinophores, and tail, are similar in both species, as is the possession of a conical penis. The animals differ externally, however, in that *F. gracilis* has longer, acutely pointed foot corners, an anus beneath the first row of the second ceratal cluster, and a gonopore located below the posterior half of the first cluster. Although both species have similar numbers of radular teeth rows, the rachidian teeth of *F. gracilis* are broader (length to width ratio), while the central cusp is shorter and narrower. Differences are also found in the reproductive anatomy of the two species, both in the shape of the receptacula seminis and in the length and number of coils of the ampulla.

It is interesting to note that these two species, *Flabellina amabilis* and *F. gracilis*, appear to occupy similar ecological niches in their respective distributional ranges. Both species are stenotrophic in their prey selection and are found associated with species of the athecate hydroid *Eudendrium* (KUZIRIAN, 1979). They share the same preferences for hard rocky substrates. They also have similar seasonal occurrences and lay identical undulating coiled egg masses (type B; HURST, 1967), which they deposit around and among the branches of their hydroid prey.

Flabellina amabilis is found sympatrically with *F. athadona* in Oshoro Bay. Because the two species are often difficult to distinguish as preserved specimens, identification of living animals is preferable for ecological investigations. Details on the ecological relationships between these two species will be reported in a later paper.

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Taxonomic and Geographical Range Data on Two Rare Species of *Okenia* (Gastropoda: Nudibranchia: Doridacea) from the Eastern Atlantic

by

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Abstract. The Atlantic species of *Okenia aspersa* Alder & Hancock, 1845, is redescribed from one specimen from southern Portugal collected during the International Marine Biological Expedition "ALGARVE-88." In addition, another rare species of *Okenia*, *O. mediterranea* (Ihering, 1886), is redescribed from specimens from southern Spain. Geographical range data for both species are included. Finally, we compare our specimens with the descriptions provided by other authors.

INTRODUCTION

Until now, the only species of the genus *Okenia* Menke, 1830, recorded from the Iberian Peninsula was *O. impexa* Marcus, 1957, found in the Cabo de Palos, Mediterranean (TEMPLADO, 1982). However, during the International Marine Biological Expedition "ALGARVE-88" (southern Portuguese coasts) (May-June 1988), organized by the MNHN of Paris (P. Bouchet) and the INIP of Portugal (L. Saldanha), one specimen of a species of *Okenia* not previously recorded from the Iberian coasts was collected: *O. aspersa* Alder & Hancock, 1845. In addition, during sampling along the southern Spanish coasts (El Portil, Huelva) in Spring 1989, 22 specimens of another species of *Okenia* that we had never seen were collected. We have concluded that these specimens belong to *O. mediterranea* (Ihering, 1886). In this paper, we present new taxonomic and geographical range data for both species.

Family GONIODORIDIDAE H. & A. Adams, 1854

Okenia Menke, 1830

Okenia aspersa Alder & Hancock, 1845

Material: One specimen, 8 mm in length, collected by SCUBA at 31 m depth in Sagres, Portugal (37°N, 8°55'W), 20 May 1988.

Description: The body bears spicules and a narrow pallial ridge with 16 simple appendages, of which the anterior 4 are elongate, while the remainder are shorter. The frontal velum is slightly bilobed (Figure 1A). The rhinophores, having 43 lamellae, are a little longer than the anterior appendages (Figure 1D). The branchial tuft has 11 unipinnate gills (Figure 1E). The spicules lie within the integument and up to the tips of the pallial ridge appendages (Figure 1C). The genital pore opens on the right of the anterior third of the animal's body.

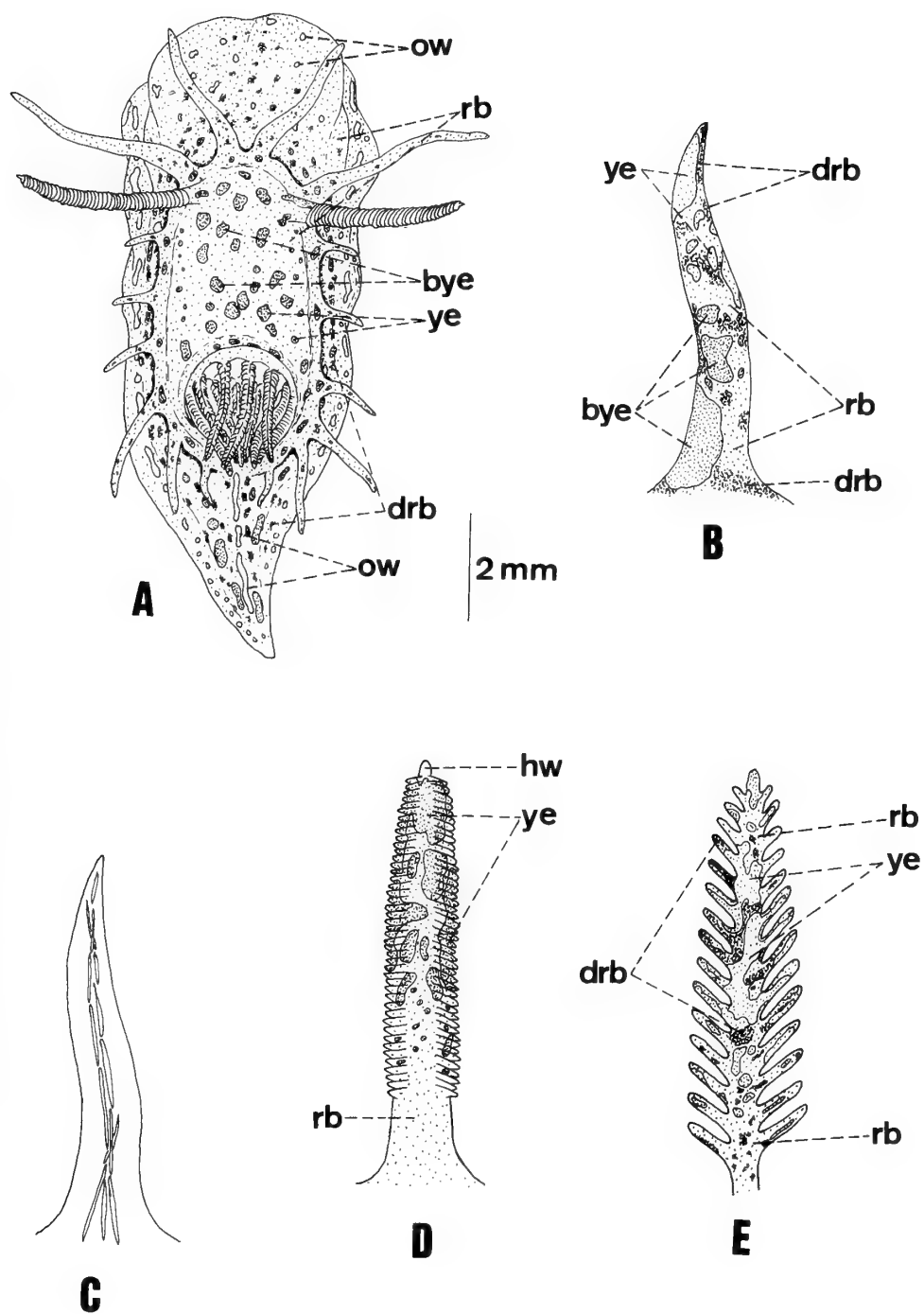


Figure 1

Okenia aspersa. A. Dorsal view of the specimen. B. Detail of one of the pallial ridge appendages. C. Arrangement of the spicules within these appendages. D. Detail of a rhinophore. E. Detail of a gill. Key: bye, bright yellow; drb, dark reddish brown; hw, hyaline white; ow, opaque white; rb, reddish brown; ye, yellow.

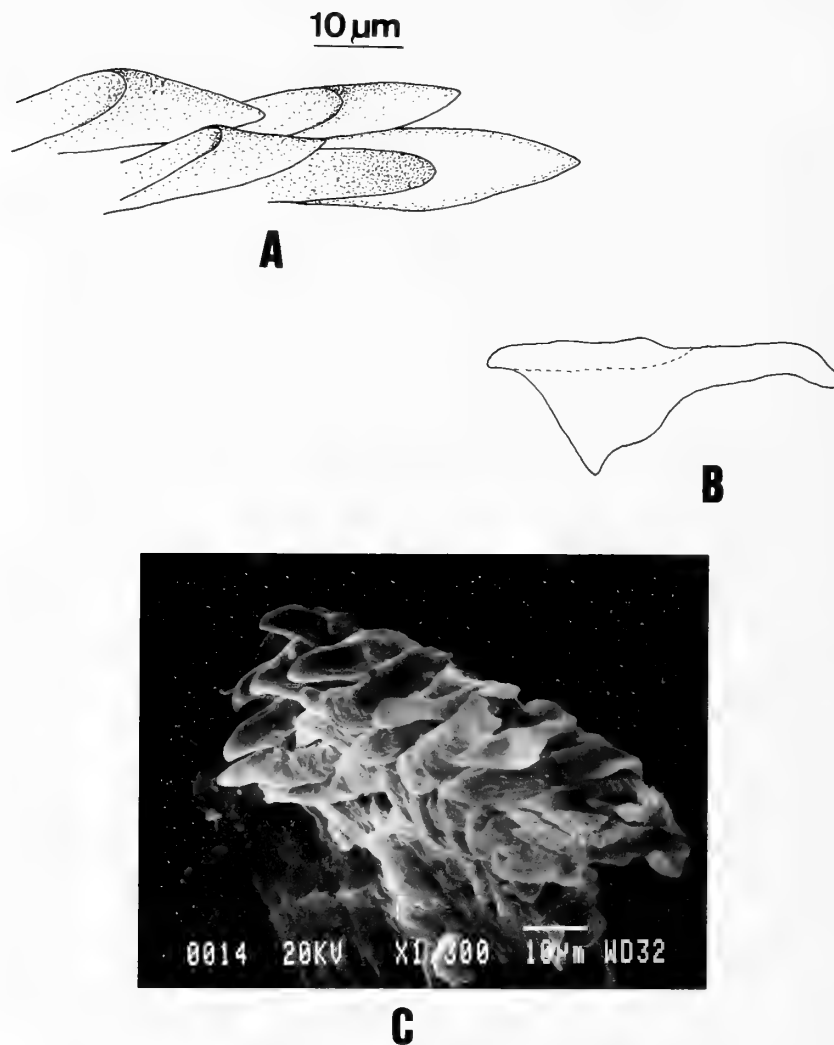


Figure 2

Okenia aspersa. A. Detail of some elements of the cuticular labial armature (drawn with a camera lucida). B. Lateral view of one of these. C. Scanning electron micrographs of these elements.

The ground color of the body, rhinophores, gills, and appendages is reddish brown. Small areas of the flanks, veil, and tail, as well as the rhinophores, gills, and appendages, display a darker color. Yellow patches, some brighter than others, exist on the rhinophores, gills, appendages, and the entire body, except the ventral surface of the foot. The tips of the rhinophores and appendages are hyaline white. Also present are small scattered opaque white spots on the flanks, veil, and tail. The tail has a white middle line from the gills to almost its tip (Figure 1A, B, D, E).

The labial cuticular armature is composed of two areas of elongate elements, which do not form a complete ring

around the mouth. These elements have a single smooth cusp and a hole on which the posterior elements lie (Figure 2A, B, C). The radular formula of the specimen is $26 \times 1.1 \cdot 0.1 \cdot 1$. The innermost teeth bear 10–12 strong denticles on the cusp, while the outermost have a prominent smooth cusp (Figure 3A, B). The reproductive system (Figure 4A) has a white ampulla, slightly curved at its distal end. The elongate and flattened prostate forms a loop and connects with a long and folded duct that ends in an elongate penis with numerous penial spines (Figure 4B, C). The gametolytic gland is spherical and opens outwardly through a long and thin vaginal duct that forms a loop before it widens in its distal region. The thin allosperm

duct starts from the gametolytic gland close to the vaginal duct. The pyriform seminal receptacle enters the allosperm duct close to the gametolytic gland.

Geographical range: *Okenia aspersa* has been recorded in Norway (THOMPSON & BROWN, 1984; JUST & EDMUNDS, 1985; PLATTS, 1985), Denmark (JUST & EDMUNDS, 1985; PLATTS, 1985), Shetlands Isles (THOMPSON & BROWN, 1984; PLATTS, 1985), British Isles (THOMPSON & BROWN, 1984; PLATTS, 1985), Atlantic France (BOUCHET & TARDY, 1976, according to THOMPSON & BROWN, 1984), and Massachusetts, USA (MORSE, 1972). So, our specimen constitutes the most southern record of this species and the first record on the Iberian Peninsula.

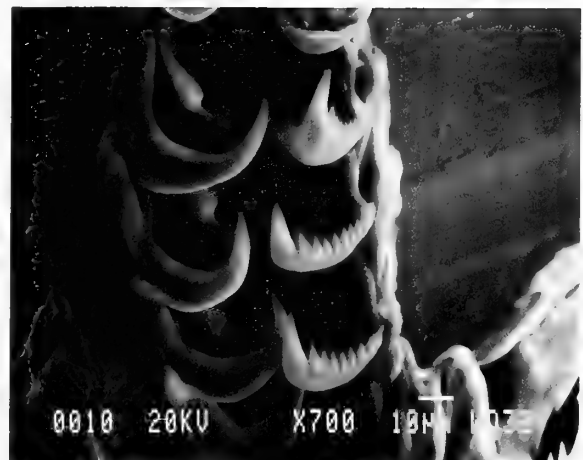
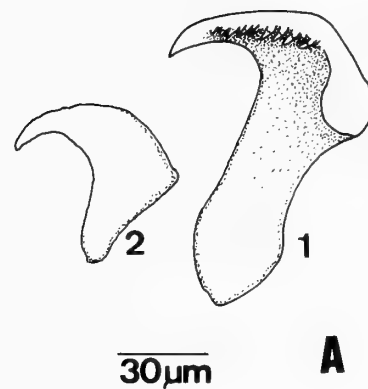
Discussion: According to Lemche (see JUST & EDMUNDS, 1985) the differences that he observed between the specimen attributed to *Okenia aspersa* and those of ALDER & HANCOCK (1845–1855) are probably due to Alder & Hancock's inaccurate description. The specimen of *O. aspersa* of THOMPSON & BROWN (1976, 1984) agrees with Alder & Hancock's description. According to JUST & EDMUNDS (1985), *O. aspersa* is clearly identical with *O. ascidicola* Morse, 1972, from Massachusetts, and, further, Lemche thought that *O. pulchella* Alder & Hancock, 1854, was conspecific with *O. aspersa*. However, MORSE (1972) compared her material with *O. pulchella* and concluded that they are different. ALDER & HANCOCK (1845–1855) described *O. pulchella* with denticulate innermost radular teeth, while THOMPSON & BROWN (1984) described smooth innermost radular teeth in a specimen attributed to this species. In addition, some authors (PRUVOT-FOL, 1954; SCHMEKEL & PORTMANN, 1982) considered *O. aspersa* conspecific with *O. quadricolor* (Montagu, 1815), but THOMPSON & BROWN (1984) reached the opposite conclusion after scrutiny of Montagu's description.

Our specimen is quite similar to those of MORSE (1972) and Lemche (see JUST & EDMUNDS, 1985), although it lacks the mid-dorsal appendage before the branchial tuft that is present in these latter. MORSE's (1972) brief description of the reproductive system does not permit its comparison with ours.

Okenia mediterranea (Ihering, 1886)

Material: (1) Seven specimens of 3.5–8.5 mm in length, collected intertidally, El Portil (Huelva, Spain) (37°12'40"N, 7°7'50"W), 6 April 1989. (2) Eleven specimens, 5–7.5 mm in length, collected intertidally, El Portil (Huelva, Spain), 23 April 1989. (3) Four specimens, 6 mm in length, collected intertidally, El Portil (Huelva, Spain), 6 May 1989.

All specimens have been deposited in the Laboratorio de Biología Marina, Departamento de Fisiología y Biología Animal, Universidad de Sevilla.



B

Figure 3

Okenia aspersa. A. Radular teeth of a half-row. B. Scanning electron micrographs of the same.

Description: The body bears spicules and a narrow pallial ridge with 18–24 appendages that are simple, except that the two most posterior appendages on each side join at their bases. The two most anterior appendages are elongate, the following two are slightly smaller, and the remaining are short and similar to each other in length. The frontal velum is slightly bilobed (Figures 5, 6A). The rhinophores have 12–20 lamellae and the two most anterior appendages are longer (Figure 6D, a and b). The branchial tuft has 5–9 unipinnate gills, which have 3–15 laminae (Figure 6E). The prominent anal papilla is located in the

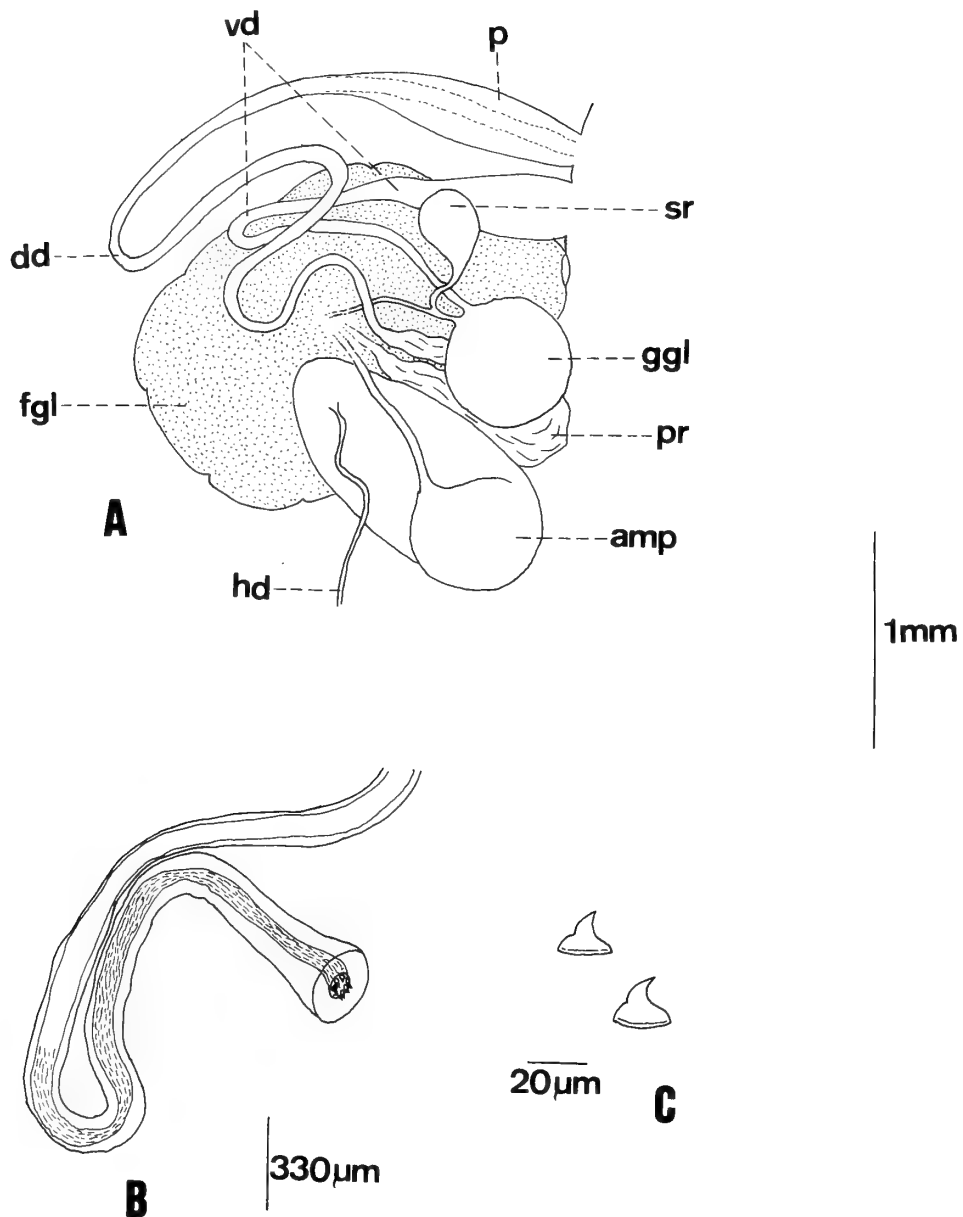
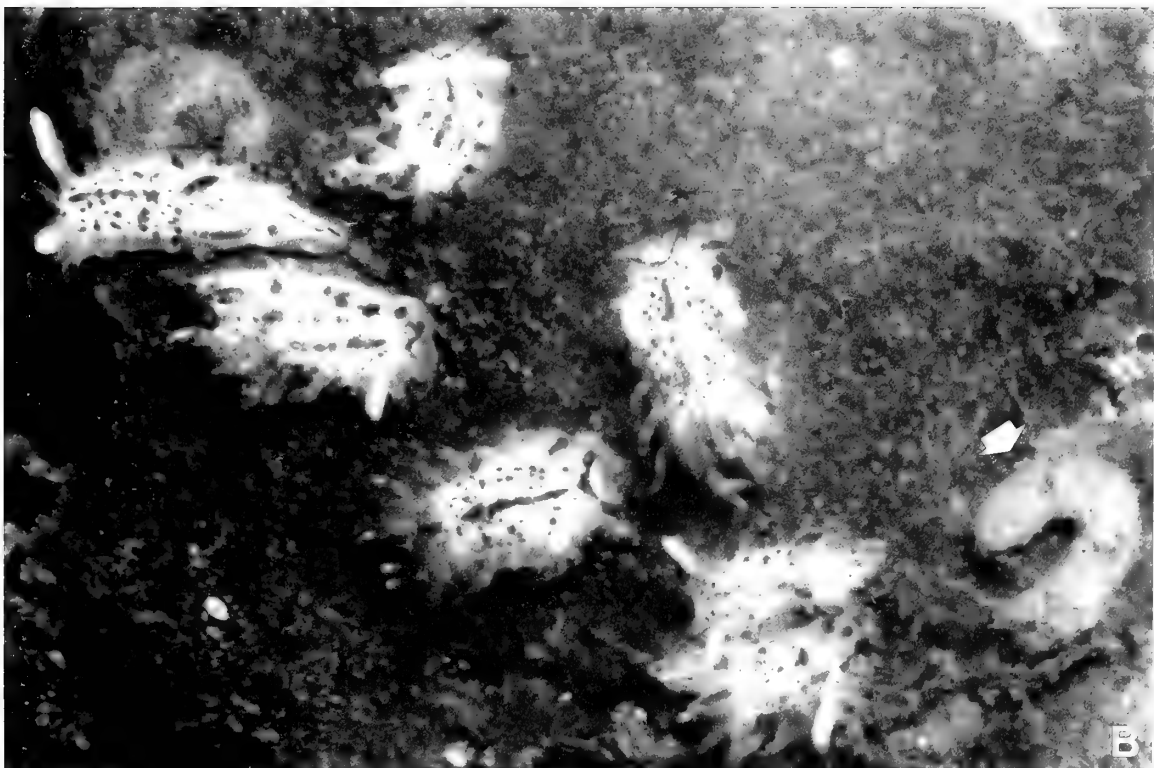


Figure 4

Okenia aspersa. A. Reproductive system. B. Detail of the penis. C. Detail of the penial spines. Key: amp, ampulla; dd, deferent duct; fgl, female gland; ggl, gametolytic gland; hd, hermaphroditic duct; p, penis; pr, prostate; sr, seminal receptacle; vd, vaginal duct.

Figure 5

Okenia mediterranea. A. Specimen 6 mm in length, 6 April 1989. B. Seven specimens, one 8 mm, five 3 mm, and one 5 mm in length, 6 April 1989, on *Alcyonidium* cf. *mytili*; arrow indicates the spawn of the species.



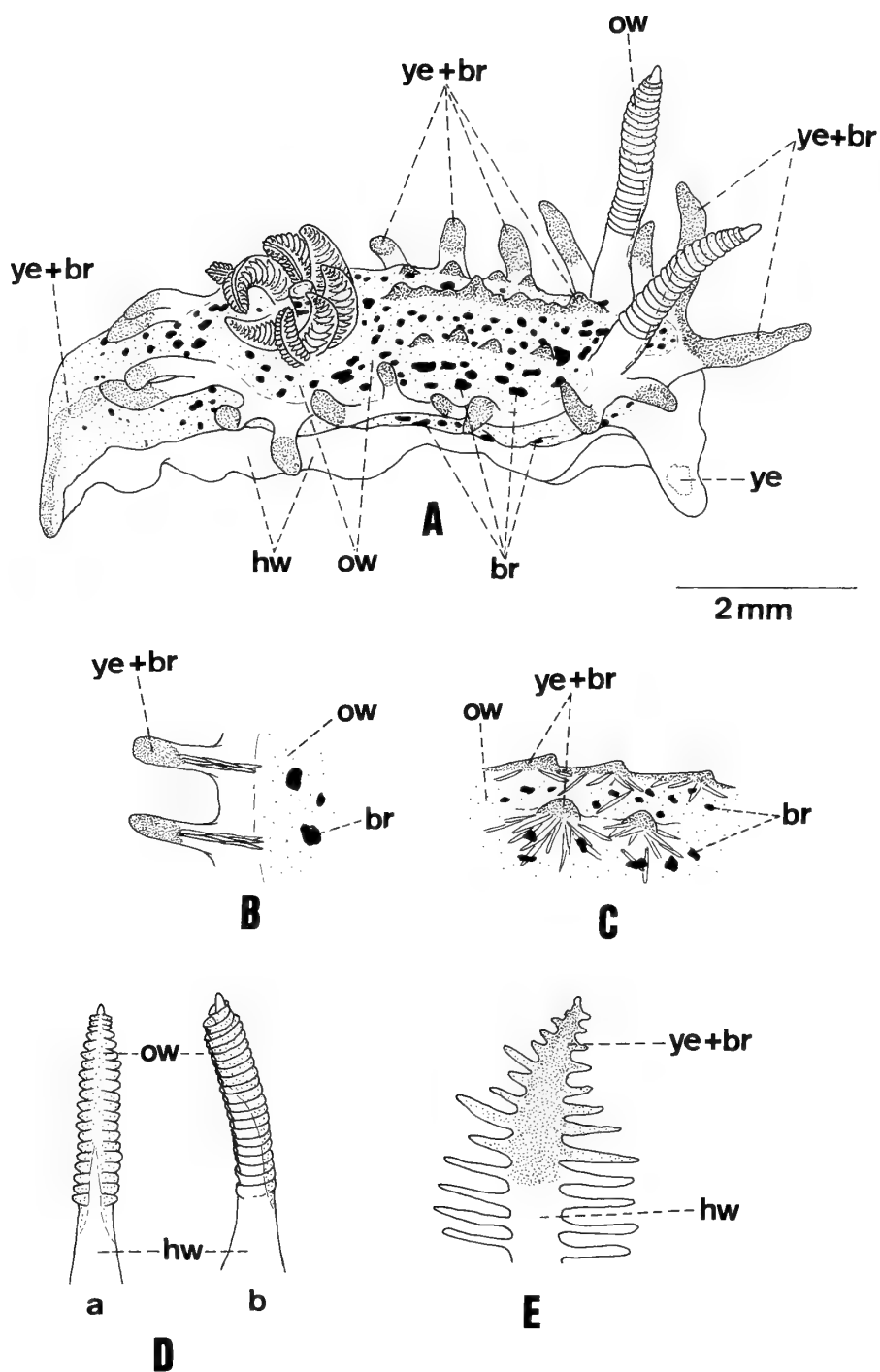


Figure 6

Okenia mediterranea. A. Dorsolateral view of one specimen. B. Arrangement of the spicules within the pallial ridge appendages. C. Arrangement of the spicules below the notal crests and elevations. D. Anterior (a) and lateral (b) view of a rhinophore. E. Detail of a gill. Key: hw, hyaline white; ow, opaque white; ye, yellow; ye + br, yellow + blood red.

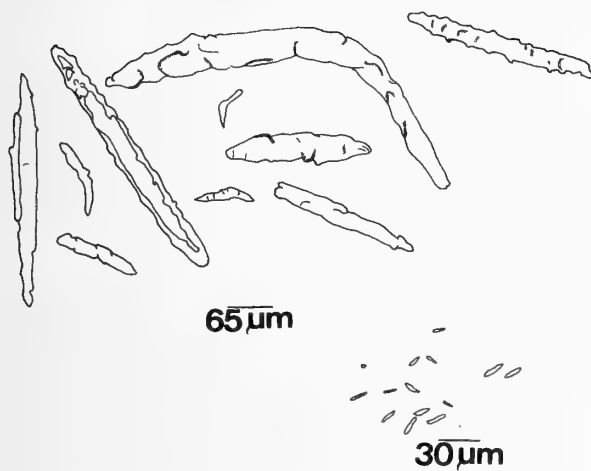


Figure 7

Okenia mediterranea. Different types of spicules observed in this species.

middle of the branchial tuft. A conspicuous keel-shaped crest formed by four elevations runs from the rhinophores towards the gills. In the same way, three or four elevations in a line (sometimes two) are usually present on both sides of this crest (Figure 6A). The spicules lie within the integument (Figure 7) and form a network in the foot and flanks of the animals. The spicules are also in the tips of the pallial ridge appendages (Figure 6B) and are arranged, in the same way, under the crest and the notal elevations (Figure 6C). The genital pore opens on the right flank of the animal, behind the rhinophoral level.

The ground color of the body (Figure 6A) is hyaline white suffused by an opaque white pigmentation that covers the dorsum and frontal veil. There is a yellow spot on the corner of each frontal velum. Yellow pigment is also on the mid-apical surface of all the appendages, the central crest, and the flanking elevations, as well as on the mid-apical surface of the gills and the middle line of the tail. Red pigment covers the yellow, except on the spots of the frontal velum. Both colors may combine to form orange. Scattered red spots of different sizes are also on the opaque white pigmentation of the dorsum, flanks, and tail of the animal. The yellow and red pigments of the two most anterior appendages almost cover their whole surface and the pallial edge that joins them, except in one 3.5-mm-long specimen. The rhinophores are hyaline white, but are covered by the above-mentioned opaque white pigmentation on their anterior faces, except on their bases, and apical third of the posterior faces (Figure 6D, a and b). The gills are hyaline white in those parts not covered by the yellow and red pigments (Figure 6E).

The internal anatomy of this species is represented in Figure 8. The labial armature is composed of two areas of elongate cuticular elements, which do not form a com-

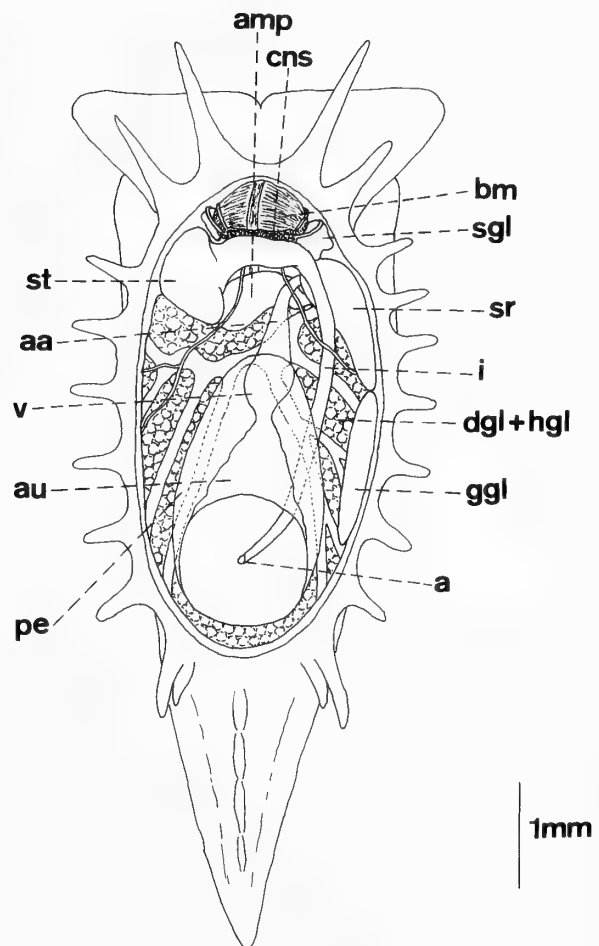


Figure 8

Okenia mediterranea. Internal anatomy. Key: a, anus; aa, anterior aorta; amp, ampulla; au, auricle; bm, buccal mass; cns, central nervous system; dgl + hgl, digestive gland + hermaphroditic gland; ggl, gametolytic gland; i, intestine; pe, pericardium; sgl, salivary gland; sr, seminal receptacle; st, stomach; v, ventricle.

plete ring around the mouth. Each element has an edge with 3–5 denticles (Figure 9A). The radular formula of one 8.5-mm-long specimen is $25 \times 1.1 \cdot 0.1 \cdot 1$. The innermost radular teeth have 28–31 small denticles on each cusp, while the outermost teeth lack denticles and possess a prominent cusp slightly hooked and curved inwards (Figure 9B, D). The reproductive system (Figure 10A) has a large, white ampulla. The prostate, elongate and flattened, forms a loop and connects with a long deferent duct that ends in an elongate, cylindrical penis with numerous penial spines (Figure 10B). The nacreous albumen gland connects with the mucous gland near the start of the prostate. The gametolytic gland is spherical and opens outwardly through a thin vaginal duct that forms two loops before widening in its distal part. The thin allosperm duct starts

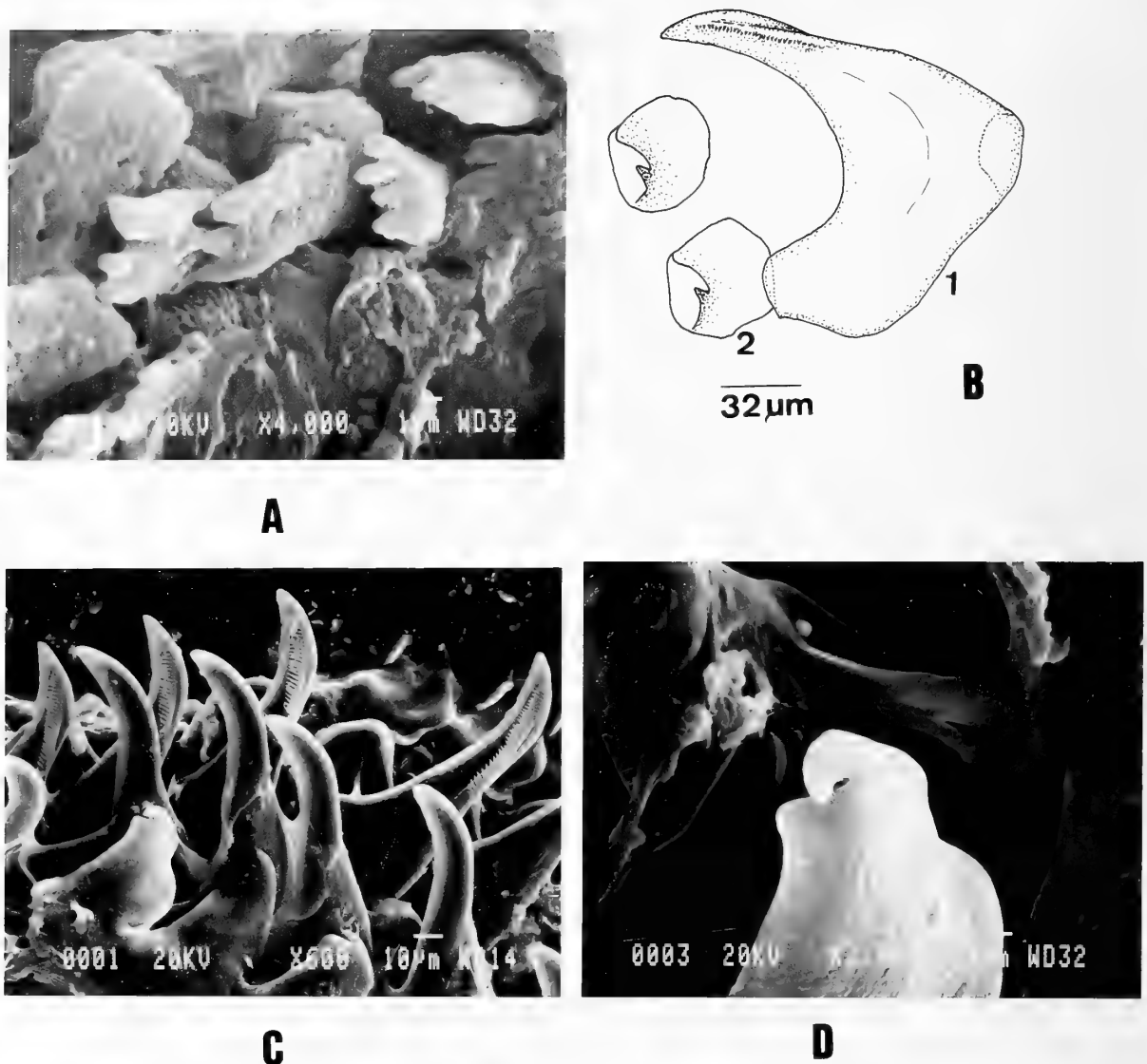


Figure 9

Okenia mediterranea. A. Scanning electron micrograph of some elements of the cuticular labial armature. B. Innermost (1) and outermost (2) radular teeth of a half-row (drawn with a camera lucida). C. Scanning electron micrograph of the radular teeth. D. Scanning electron micrograph of a detail of the cusp of an outermost tooth.

from the gametolytic gland close to the vaginal duct. The seminal receptacle joins the allosperm duct close to the gametolytic gland.

Biology: All specimens were found on the ctenostomate bryozoan *Alcyonidium* cf. *mytili* Dalyell, 1848. Some egg masses of this species were collected on this substrate and others were observed in the laboratory. The spawn is a semicircular string (Figure 5B), circular in section, and in some cases the spawn almost forms a ring. The diameter is about 1 mm and the strings have a length of 10–12 mm. Each capsule contains one egg. The eggs are almost spher-

ical and white. The diameter of the capsules is 71.5–97.5 µm and that of the eggs is 58.5–78 µm.

Geographical range: *Okenia mediterranea* has previously been recorded at its type locality, Naples, Italy, in the Mediterranean (IHERING, 1886; SCHMEKEL, 1979; SCHMEKEL & PORTMANN, 1982). Our specimens constitute the first record of this species from the Atlantic Ocean and the Iberian Peninsula.

Discussion: Although our specimens differ slightly from the specimens of *Okenia mediterranea* from Naples

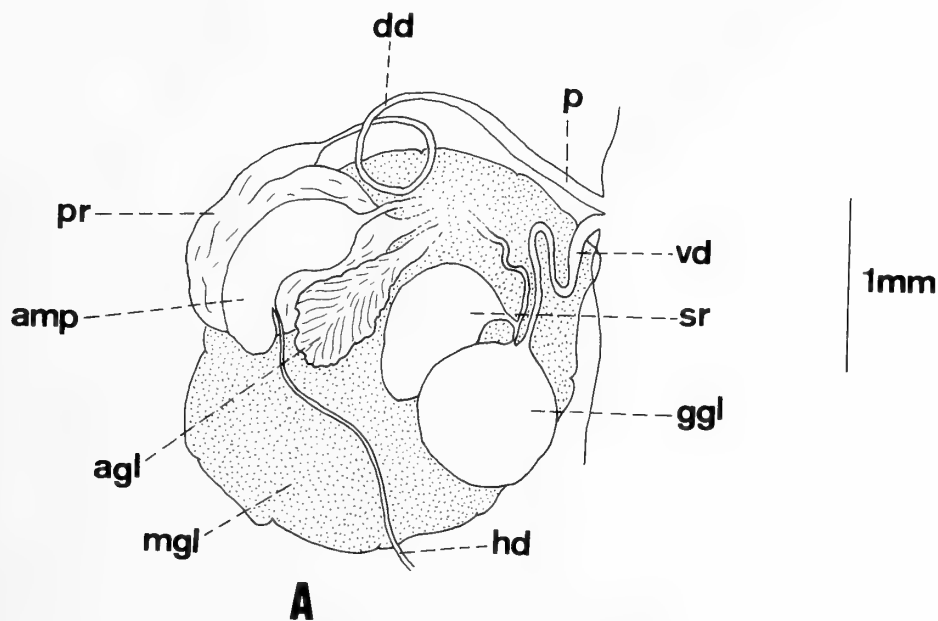
**B**

Figure 10

Okenia mediterranea. A. Reproductive system. B. Scanning electron micrograph of the penis. Key: amp, ampulla; agl, albumen gland; hd, hermaphroditic duct; mgl, mucous gland; p, penis; pr, prostate; sr, seminal receptacle; vd, vaginal duct.

(IHERING, 1886; SCHMEKEL, 1979; SCHMEKEL & PORTMANN, 1982), we prefer provisionally to consider our specimens as belonging to this species. SCHMEKEL (1979) corrects her own record of specimens of *O. amoenula* Bergh, 1907 (SCHMEKEL, 1968), which really correspond to *O. mediterranea*, and discusses the differences between the two

species. SCHMEKEL (1979) reports the differences between her specimens of *O. mediterranea* and those described by IHERING (1886), emphasizing the contradictions of this author when he described the species: for example, Ihering wrote that the mantle was smooth, but drew two tubercles on each side of the median crest. However, IHERING (1886)

did not mention the unpaired ceras located behind the gills that was described by SCHMEKEL (1979). We agree with Schmekel that the specimen attributed to this species by PRUVOT-FOL (1951, 1954) corresponds neither to *O. amoenula* nor *O. mediterranea*.

The descriptions of the *Okenia mediterranea* specimens from Naples do not specify clearly whether the body pigmentation is white hyaline suffused by an opaque white or whether the body lacks this latter. Moreover, the arrangement of the red pigmentation of the notum of our specimens is slightly different from that on the specimens of Naples. The red and yellow colors of the appendages of Atlantic specimens cover at most the apical half, while in the Mediterranean specimens they cover almost their entire length. These latter specimens have rhinophores that are completely opaque white, while ours do not. Other differences between the Mediterranean specimens and ours are the presence of three or four elevations in a line on both sides of the median crest and the absence of the unpaired ceras behind the gills observed in some of the specimens of SCHMEKEL (1979) and SCHMEKEL & PORTMANN (1982). The base of the innermost radular teeth of our specimens is broader than in Schmekel's specimens. This variability could be due to the observation of the radular teeth with a little variation in their arrangement (for instance, see the differences that can be observed between the radular teeth of the same specimen of *Okenia aspersa* in Figure 3A, B).

The incomplete description of the reproductive system of Schmekel's specimens (SCHMEKEL, 1979), as well as the absence of drawings in Ihering's and Schmekel's descriptions of this system do not permit a good comparison with that described in this paper.

SCHMEKEL (1979) points out that the situs of this system in her specimens "corresponds in the main features with the situs of *Okenia amoenula* Bergh, 1907 (MACNAE, 1958: fig. 23)," and she does not find differences between the reproductive systems of the two species. However, comparing the reproductive system of our specimens with that of *O. amoenula*, differences can be observed: the prostate of our specimens is broader and shorter than in *O. amoenula*, the joint of the seminal receptacle with the allosperm duct is closer to the gametolytic gland in our specimens, and the seminal receptacle of our animals is different in size (larger) and shape (not pyriform).

In addition to having these differences in the reproductive system, *Okenia amoenula* has smooth elements on the labial armature (BERGH, 1907) and different coloration. Thus, we conclude that our material belongs to a different species. Despite the impossibility of comparing the reproductive system of our specimens with that of the material from Naples, we consider them both provisionally as *O. mediterranea*.

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New Early Eocene Species of *Arca* s.s. (Mollusca: Bivalvia) from Southern California

by

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Abstract. Two new species of the warm-water marine bivalve *Arca* s.s. are reported from the early Eocene of Ventura County, southern California. They represent the earliest species of *Arca* s.s. known from the Pacific coast of North America.

Arca (*Arca*) *filewicz*i sp. nov. is from the early early Eocene part of the "Meganos Stage" in the upper Santa Susana Formation, north side of Simi Valley, southern California.

Arca (*Arca*) *givensi* sp. nov., a previously unnamed species from the middle early Eocene "Capay Stage," part of the Juncal Formation, Pine Mountain area, southern California, is now named and described.

INTRODUCTION

The living arcid bivalve *Arca* s.s. has worldwide distribution in tropical and warm seas (REINHART, 1935). There is no agreement as to when *Arca* s.s. first appeared in the fossil record. It has been reported from strata of Early Cretaceous age in southern England (WOODS, 1899; REINHART, 1935; CASEY, 1961:605). NEWELL (1969), however, reported its geologic range to be Late Cretaceous to Recent.

Arca s.s. does not show up in the fossil record of the Pacific coast of North America until early Eocene time, based on my recent discovery of *A. (A.) filewicz*i sp. nov. in rocks of this age in southern California. Because this new species has no Cretaceous or Paleocene ancestral species of *Arca* s.s. in the Pacific coast region of North America (REINHART, 1943; MOORE, 1983), it must have immigrated into southern California. Like many other Old World mollusks that immigrated into southern California during the early Eocene, the route of migration was most likely by way of Central America (SQUIRES, 1987). The time of arrival of *Arca* s.s. into California coincided with a worldwide warming trend (HAQ, 1981).

Previously, the earliest record of *Arca* s.s. from the Pacific coast of North America was *A. (A.)* n. sp.? Givens, 1974, from strata of middle early Eocene age, southern California. This species is herein named and described as *A. (A.) givensi* sp. nov.

The terms "Meganos Stage" and "Capay Stage" used in this report refer to Pacific coast of North America provincial megainvertebrate stages as used by SAUL (1983)

who regarded the "Meganos Stage" as late Paleocene to early early Eocene and the restricted "Capay Stage" of GIVENS (1974) as middle early Eocene.

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCR, University of California, Riverside.

STRATIGRAPHIC OCCURRENCES AND GEOLOGIC AGES

*Arca (A.) filewicz*i was found in the upper part of the Santa Susana Formation at locality CSUN 965 (Figure 1) at 518 m (1700 ft) elevation, on the east side of an abandoned oil-well road long the west side of a ridge, 137 m (450 ft) south and 792 m (2600 ft) east of the northwest corner of section 32, T3N, R17W, Santa Susana quadrangle (7.5 minute), 1951, north side of Simi Valley, Ventura County, California. The locality is about 100 m stratigraphically below the basal conglomerate of the Llajas Formation, which disconformably overlies the Santa Susana Formation. No age-diagnostic microfossils have ever been found in this part of the Santa Susana Formation. Earliest Eocene calcareous nannofossils, however, have been found in the immediately underlying strata, and using this information FILEWICZ & HILL (1983:fig. 5) assigned an early Eocene age (CP9 Zone of OKADA & BUKRY, 1980) to the upper 100 m of the Santa Susana Formation on the north side of Simi Valley. This age is equivalent to the

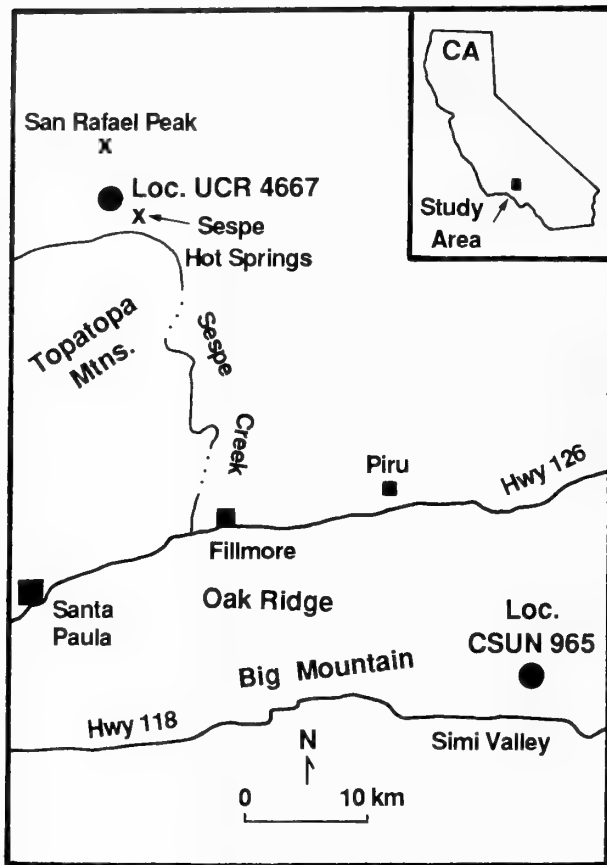


Figure 1

Geographic occurrences of two new species of early Eocene *Arca* s.s. in southern California.

early early Eocene part of the "Meganos Stage," and SAUL (1983) assigned the upper 100 m of the Santa Susana Formation on the north side of Simi Valley to this stage.

Two specimens of *Arca* (*A.*) *filewiczii* were found, and one is complete. They are from a lens of greenish gray, very fine sandstone surrounded by sandy siltstone. Associated macrofossils were abundant specimens of the gastropod *Turritella andersoni susanae* Merriam, 1941, and rare specimens of the brachyuran crabs *Cyclocorystes aldersoni* Squires, 1980, and *Zanthopsis hendersonianus* Rathbun, 1926. The fossils in the lens are interpreted to be a very slightly transported assemblage in a relatively shallow offshore environment. This interpretation is in agreement with what HEITMAN (1983) found on the basis of his paleoecologic study of benthic foraminifers from this formation. He discovered that although paleobathymetry for the Santa Susana Formation on the north side of Simi Valley was mostly restricted to the bathyal realm, the upper part represents a shoaling event associated with basin filling that deposited silty sandstone just above the shelf-slope break.

Arca (*A.*) *givensi* was found in the lower part of the

Juncal Formation at locality UCR 4667 (Figure 2) at 1097 m (3600 ft) elevation, on the east side of a south-draining tributary to Hot Springs Canyon, 518 m (1700 ft) south and 427 m (1400 ft) east of the northwest corner of section 21, T6N, R20 W, Topatopa Mountains quadrangle (7.5 minute), 1943, Ventura County, California (GIVENS, 1974). The locality is about 53 m stratigraphically above the base of the Juncal Formation, and GIVENS (1974) assigned this part of the Juncal Formation to the *Turritella wasana infera* fauna of the middle early Eocene "Capay Stage."

Nineteen specimens of *Arca* (*A.*) *givensi* were found, and all are single valves. They are from a greenish gray sandstone bed within a predominantly mudstone facies. Associated macrofossils listed by GIVENS (1974:table 1) are other bivalves and some gastropods, including *Turritella andersoni* Dickerson, 1916. GIVENS (1974) interpreted that the rocks surrounding locality UCR 4667 were deposited in a nearshore, tropical or subtropical shallow-marine environment.

SYSTEMATIC PALEONTOLOGY

Family ARCIDAE Lamarck, 1809

Subfamily ARCINAE Lamarck, 1809

Genus *Arca* Linné, 1758

Type species: By subsequent designation (SCHMIDT, 1818), *Arca noae* Linné, 1758, ICZN Opinion 189, 5 October 1944.

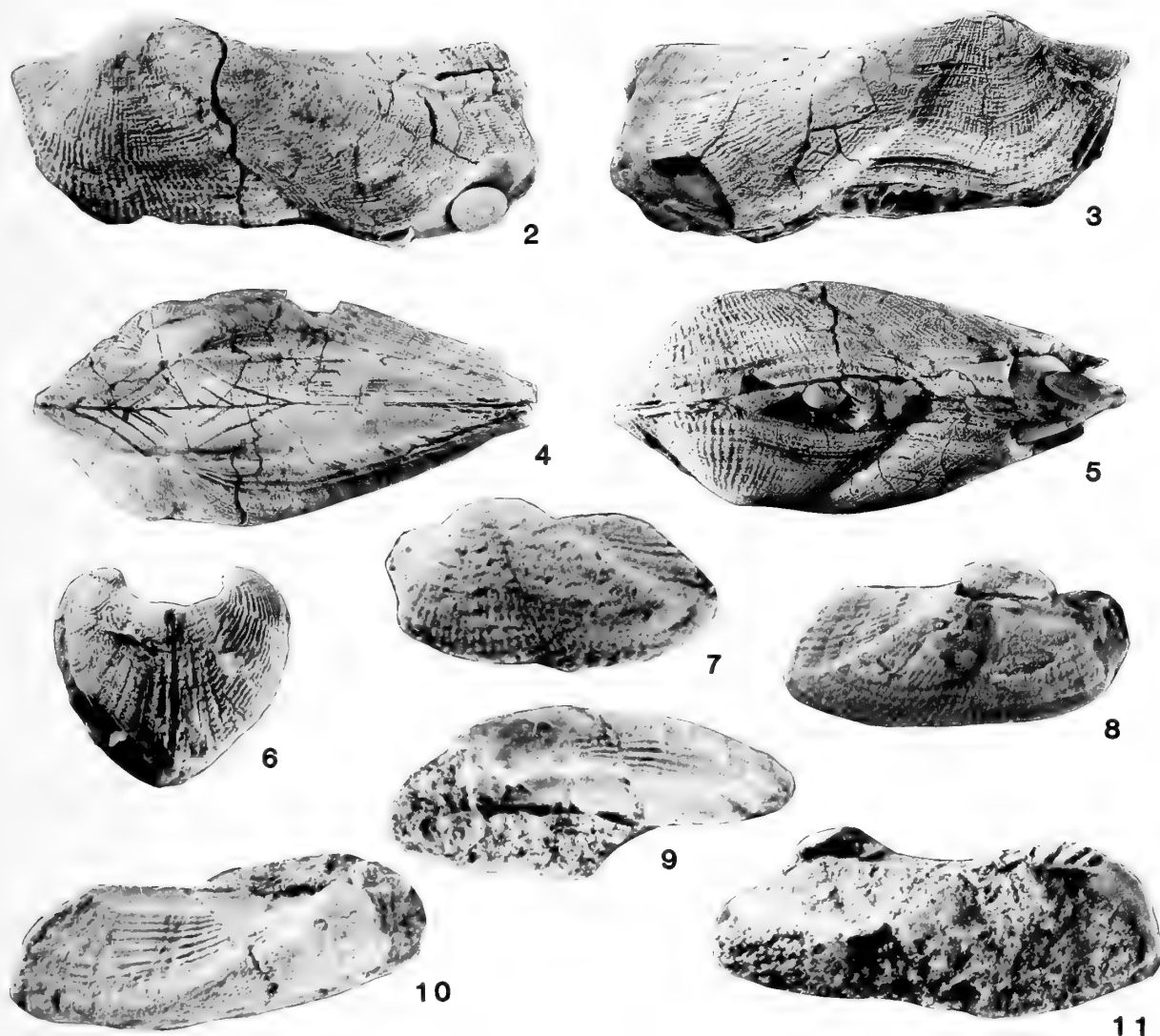
Subgenus *Arca* s.s.

Arca (*Arca*) *filewiczii* Squires, sp. nov.

(Figures 2–6)

Diagnosis: Medium size, with a weak posterior umbonal flexure, two to three radial bands on post-umbonal slope, and slightly concave ligamental area with four chevron-shaped grooves.

Description: Medium size, rhombic, very inequilateral, umbones prominent, beaks approximately one-fourth of length of shell from anterior end. Weak posterior umbonal flexure. Anterior margin parallel with posterior margin, both meeting straight hinge line at a nearly 90° angle. Ventral margin straight. Entire shell U-shaped in profile. Ligamental area extremely wide, slightly concave in umbonal area and slightly convex in posterior region of shell. Ligamental area with four chevron-shaped grooves in vicinity of beak, smooth posteriorly. Ligamental area on each valve subrectangular in shape, widest just posterior of beak. Medial sulcus from umbonal area to posterior end of byssal sinus on ventral surface of each valve; growth lines on right valve more deflected by the sinus than on left valve. Shell with fine cancellate sculpture; two to three fairly prominent radial bands on post-umbonal area. Radial ribs also di-



Explanation of Figures 2 to 11

Figures 2 to 6. *Arca (Arca) filewiczzi* Squires, sp. nov., holotype, LACMIP 8365, locality CSUN 965, $\times 1.2$. Figure 2: left valve. Figure 3: right valve. Figure 4: dorsal view. Figure 5: ventral view. Figure 6: anterior view.

Figures 7 to 11. *Arca (Arca) givensi* Squires, sp. nov., locality UCR 4667. Figure 7: paratype, UCR 4667/132, left valve, $\times 10$. Figure 8: holotype, UCR 4667/131, right valve, $\times 6.9$. Figures 9-11: paratype, UCR 4667/133. Figure 9: dorsal view, $\times 5.8$. Figure 10: oblique dorsal view, $\times 5.8$. Figure 11: interior, $\times 6.2$.

rectly beneath beaks, extending a small distance onto ligamental area.

Holotype: LACMIP 8365.

Type locality: Locality CSUN 965, north side of Simi Valley, Ventura County, southern California.

Paratype: LACMIP 8366.

Dimensions: Of holotype, height 24 mm, length 59 mm, single-valve thickness 13 mm; of paratype, height 8 mm, length 11 mm (incomplete), single-valve thickness 3 mm.

Discussion: The morphologic characteristics of *Arca* s.s. have been described by REINHART (1935) and NODA (1966). Some of the most important of these are a wide ligamental area and an elongate posterior region with a depressed area between the hinge line and umbonal flexure. The new species has all of the requisite external characters. Unfortunately, no internal features could be observed without destroying the only two specimens of the new species. The match of external morphology, however, is sufficient to assign the new species to *Arca* s.s.

Arca (A.) filewiczzi most resembles *A. (A.) biangula* LA-

MARCK (1805: 219; 1807: pl. 17, figs. 2a, b, expl. p. 238; PALMER, 1977: pl. 24, figs. 5a, b, c; COSSMANN & PISSARRO, 1904-1906: pl. 35, fig. 110-1; BRITISH MUSEUM (NATURAL HISTORY), 1975: pl. 6, fig. 10) from early Eocene (Cuisian Stage) through late Eocene (Bartonian Stage) strata in the Paris Basin, France, and Hampshire Basin, southern England. *Arca* (*A.*) *filewicz* was compared to a specimen of *A.* (*A.*) *biangula* from the UCMP Cloez collection of Paris Basin Paleogene mollusks, as well as to published figures of *A.* (*A.*) *biangula*. These comparisons revealed that *A.* (*A.*) *filewicz* differs from *A.* (*A.*) *biangula* in the following features: much weaker posterior umbonal flexure, beaks one-fourth rather than one-third of length of shell from anterior end, fewer and less prominent radial ribs on post-umbonal slope, four rather than six chevron-shaped grooves in ligamental area, chevron-shaped grooves confined to beneath umbonal area rather than throughout ligamental area, ligamental area on each valve more rectangular in shape rather than triangular, and a much smaller byssal gape.

Arca (*A.*) *filewicz* differs from *A.* (*A.*) *givensi* in the following features: six times larger, much weaker posterior umbonal flexure, beaks one-fourth rather than one-third of length of shell from anterior end, anterior and posterior margins both meet hinge line at a nearly 90° angle rather than curve to meet the hinge line, fewer and less prominent radial ribs on post-umbonal slope, four rather than one chevron-shaped groove in ligamental area, and a much more prominent byssal sinus on each valve.

On the basis of recent work by MOORE (1983), the only other Eocene *Arca* s.s. known from the Pacific coast of North America is *A.* (*A.*) *hawleyi* REINHART (1943:21-22, pl. 2, figs. 19-22) from late Eocene "Tejon Stage" strata in southern California (REINHART, 1943; WEAVER & KLEINPELL, 1963). *Arca* (*A.*) *filewicz* differs from *A.* (*A.*) *hawleyi* in the following features: shell does not narrow posteriorly, weaker commarginal ribs, and four rather than three chevron-shaped grooves in ligamental area.

Etymology: The species is named for M. V. Filewicz for his long-term cooperation in providing calcareous nanofossil age dates for many Paleogene formations on the Pacific coast of North America.

Occurrence: Early early Eocene part of the "Meganos Stage," upper Santa Susana Formation, north side of Simi Valley, Ventura County, southern California, locality CSUN 965.

Arca (*Arca*) *givensi* Squires, sp. nov.

(Figures 7-11)

Arca (*Arca*) n. sp.? GIVENS, 1974: 40, pl. 1, fig. 8.

Diagnosis: Small size, with a strong posterior umbonal flexure, six to eight primary ribs on post-umbonal slope, and a flattish ligamental area with one chevron-shaped groove.

Description: Small size, rhombic, very inequilateral, umbones prominent, beaks approximately one-third of length of shell from anterior end, beaks overhang ligamental area. Strong carina-like posterior umbonal flexure. Anterior margin parallel with posterior margin, both curving toward straight hinge line. Ventral margin fairly straight. Ligamental area flat throughout, with one chevron-shaped groove in vicinity of beak, smooth elsewhere. Ligamental area widest opposite beak. Slight medial sulcus from umbonal area to center of ventral margin of each valve where there appears to be a slight byssal sinus. Shell with fine to fairly strong cancellation ornamentation. Radial ribbing strongest on post-umbonal slope with six to eight fairly strong radial ribs, interspaces with no interribs or with one or more interribs, the number increasing ventrally. Only portions of dentition observed; small, numerous teeth below beak and at least four large elongate teeth on posterior end.

Holotype: UCR 4667/131 (formerly UCR hypotype 4667/131).

Type locality: Locality UCR 4667, Pine Mountain area, Ventura County, southern California.

Paratypes: UCR 4667/132 and 4667/133.

Dimensions: Of holotype, height 3 mm, length 7 mm, single-valve thickness 1.5 mm; of paratype, UCR 4667/132, height 2 mm, length 4.5 mm, single-valve thickness 1 mm; of paratype, UCR 4667/133, height 4.5 mm, length 10 mm, single-valve thickness 2 mm.

Discussion: Nineteen specimens of the new species were collected by GIVENS (1974). Eight are right valves, seven are left valves, and four are fragments. No complete specimens were found. All of the specimens are small, and they may represent juveniles.

The external morphologic features of this new species, as well as the very small part of the dentition area that could be observed, match those described by NODA (1966) for *Arca* s.s.

Arca (*A.*) *givensi* is most similar to *A.* (*A.*) *hatchetigbeensis* HARRIS (1897:47, pl. 7, figs. 10-10a; TOULMIN, 1977:183-184, pl. 11, figs. 9-10) from the early Eocene Hatchetigbee Formation in southwestern Alabama (TOULMIN, 1977). *Arca* (*A.*) *givensi* differs from *A.* (*A.*) *hatchetigbeensis* in the following features: half the size, six to eight rather than only two radial ribs on the post-umbonal slope, and one rather than two chevron-shaped grooves in the ligamental area.

Arca (*A.*) *givensi* is also similar to *A.* (*A.*) *merriami* (VAN WINKLE, 1918:pl. 81, pl. 6, fig. 1; CLARK, 1925:80, pl. 13, figs. 5-8; WEAVER, 1943:pl. 66-67, pl. 11, fig. 8, pl. 12, figs. 3, 6-9, 12, 15) from Oligocene strata in the Grays Harbor area of southwestern Washington. *Arca* (*A.*) *givensi* differs from *A.* (*A.*) *merriami* in the following features: half the size, beaks approximately one-third rather than one-fourth of length of shell from anterior end, more

prominent radial ribs on post-umbonal slope, and presence of cancellate sculpture. *Arca* (A.) *merriami* closely resembles *A.* (A.) *washingtoniana* Dickerson, 1917, from Oligocene strata in southwestern Washington, and EFFINGER (1938) considered them to be the same species.

Arca (A.) *givensi* differs from *A.* (A.) *filewiczii* in the following features: one-sixth the size, much stronger posterior umbonal flexure, beaks one-third rather than one-fourth of length of shell from anterior end, anterior and posterior margins both curve to meet hinge line rather than intersect it at a nearly 90° angle, twice as many and less prominent radial ribs on post-umbonal slope, one rather than four chevron-shaped grooves in the ligamental area, and a much less obvious byssal sinus on each valve.

Etymology: The new species is named for C. R. Givens for this valuable contributions on Paleogene marine mollusks of North America. He also found the specimens of the new species.

Occurrence: Middle early Eocene "Capay Stage" *Turritella uvasana infera* fauna of the Juncal Formation, Pine Mountain area, Ventura County, southern California, locality UCR 4667.

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New Morphologic and Stratigraphic Data on *Calyptogena (Calyptogena) gibbera* Crickmay, 1929 (Bivalvia: Vesicomysidae) from the Pliocene and Pleistocene of Southern California

by

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Abstract. The dentition of the fossil vesicomysid marine bivalve *Calyptogena (Calyptogena) gibbera* Crickmay, 1929a, previously has not been described, and the holotype is missing and presumed lost. Recent discovery of specimens from the original lot now allows for complete description and illustration of this species, as well as for the designation of a lectotype. Comparison with other fossil and Recent *Calyptogena* from the northeastern Pacific reveals that *C. (C.) lasia* Woodring, 1938, is a junior synonym of *C. (C.) gibbera*. The geologic range of *C. (C.) gibbera* is now early Pliocene to middle Pleistocene, and the species is confined to the Los Angeles and Ventura basins, southern California.

INTRODUCTION

Three species of the vesicomysid marine bivalve *Calyptogena* have been reported from the fossil record of southern California. They are *C. (Calyptogena) pacifica* Dall, 1891, *C. (C.) gibbera* Crickmay, 1929a, and *C. (C.) lasia* (Woodring, 1938). They are all from Pliocene to Pleistocene strata. Hinge dentition is essential in the recognition of species of *Calyptogena*, but the hinge dentition of *C. (C.) gibbera* was unknown. Although CRICKMAY (1929a:fig. 1) figured the right-valve exterior of his species *Calyptogena (C.) gibbera*, he did not figure nor describe the dentition. His figured specimen, which was designated as a holotype (un-numbered), was not stored in a repository, and, to date, the specimen has not been found. Unfortunately, new material from the type locality on Deadmans Island, San Pedro Bay, southern California, can never be collected because the island was destroyed in 1928 in order to widen the main channel into the inner harbor of Los Angeles Harbor (WOODRING *et al.*, 1946; WEINSTEIN, 1967).

Without any diagnostic morphologic criteria available for *Calyptogena (C.) gibbera*, paleontologists have been unable to report any other occurrences of this species. Re-

cently, however, George L. Kennedy of the Natural History Museum of Los Angeles County Invertebrate Paleontology Section brought to my attention that the museum has 16 specimens of *C. (C.) gibbera* that Crickmay collected and identified from the type locality of his species (equivalent to locality LACMIP 30252). The specimens are also most probably from the original lot. The purpose of this article is to illustrate the hinge dentition of *C. (C.) gibbera*, based on the discovery of these very important specimens. This information will be essential in any future study of the evolutionary history of this interesting genus, which can be an important faunal member of Recent deep-sea hydrothermal vent communities (BOSS & TURNER, 1980) and of Recent and Tertiary cold-seep communities related to subduction zones (OHTA & LAUBIER, 1987; KANNO *et al.*, 1989; NIITSUMA *et al.*, 1989; GOEDERT & SQUIRES, in press).

Abbreviations used for catalog and/or locality numbers are: LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; USGS, United States Geological Survey; USNM, United States National Museum.

SYSTEMATIC PALEONTOLOGY

Family VESICOMYIDAE Dall & Simpson, 1901

Genus *Calyptogena* Dall, 1891Type species: By monotypy, *Calyptogena pacifica* Dall, 1891.Subgenus *Calyptogena* s.s.*Calyptogena* (*Calyptogena*) *gibbera* Crickmay, 1929a

(Figures 1–4)

Calyptogena gibbera CRICKMAY, 1929a:93, fig. 1; 1929b:623; WOODRING *et al.*, 1946:83; BERNARD, 1983:50.*Calyptogena* (?*Calyptogena*) *gibbera* Crickmay: BOSS & TURNER, 1980:186.*Phreagena lasia* WOODRING, 1938:50–52, text-fig. 2a, pl. 5, figs. 3–4.*Calyptogena lasia* (Woodring): WINTERER & DURHAM, 1962:295, 302, 307, 308; BOSS, 1968:739.*Calyptogena* (*Phreagena*) *lasia* (Woodring): KEEN, 1969:N664, figs. E138 10a, b.*Calyptogena* (*Calyptogena*) *lasia* (Woodring): BOSS & TURNER, 1980:187.

Original descriptions: *Calyptogena* (*C.*) *gibbera*—"This new form is to be distinguished from the living type by its outline and proportions: length 52 mm, height 29 mm, diameter 15 mm. The new species somewhat resembles *C. elongata* but has a greater height and an arched post-umbonal slope, whence the trivial name. All the dimensions, but especially the length, are greater than those of *C. pacifica*." (CRICKMAY, 1929a:93)

Calyptogena (*C.*) *lasia*—"Moderately large, elongate, thick-shelled. Lunule absent; escutcheon long, abruptly angulated and flattened. Sculpture consisting of strongly defined growth lines. Hinge of right valve consisting of a short, weak anterior cardinal, a heavy bifid middle cardinal, and a bifid posterior cardinal. Hinge of left valve consisting of a heavy anterior cardinal, joined to a heavy bifid middle cardinal, and a posterior cardinal. Adductor and pedal muscle scars deep sunk. Pallial line apparently simple." (WOODRING, 1938:50)

Discussion: Of the 16 specimens of *Calyptogena* (*C.*) *gibbera* in the LACMIP collection, four are left valves, six are right valves, and six are articulated. All of the single valves show dentition. Two of the articulated specimens show the dentition of both valves, and one of the articulated specimens shows the dentition of one valve. They are mostly fairly well preserved, especially with regard to the dentition, and one of these specimens (LACMIP 8400) is herein designated as the lectotype of *C. (C.) gibbera*. The lectotype is close in size to that of the missing and presumed lost holotype. The dimensions of the lectotype are length 50.5 mm, height 25.5 mm, and width (=diameter) approximately 6.5 mm. Two of the other topotypes are figured (Figures 1, 2) in this present report and are now hypotypes, LACMIP 8398 and 8399. The other 13 specimens are topotypes and are stored in the LACMIP col-

lection under locality LACMIP 30252 in the Pleistocene invertebrate fossil cabinets.

A comparison of the dentition and shell shape of *Calyptogena* (*C.*) *gibbera* with other species of *Calyptogena* reveals that the fossil *C. (C.) lasia* (WOODRING, 1938:50–52, text-fig. 2a, pl. 5, figs. 3, 4) is a junior synonym of *C. (C.) gibbera*, based on the examination of the holotype of *C. (C.) lasia* and the examination of 38 specimens of *C. (C.) lasia* (identified by Woodring) from locality LACMIP 21363 in the Towsley Formation, Ventura County, which is discussed below. For documentation of this determination, compare Figures 1–4 of *C. (C.) gibbera* with Figures 5–8 of *C. (C.) lasia*.

CRICKMAY's (1929a) description of *Calyptogena* (*C.*) *gibbera* is inadequate because it consists of only a brief comparison of his species to some other species of this genus. WOODRING's (1938) description of *C. (C.) lasia* is much more complete and, therefore, is also given above. Nevertheless, there are some variations in morphology that WOODRING (1938) did not mention. The right valve middle cardinal and posterior cardinal vary in the strength of how bifid they can be—namely, from fairly well developed to weak. In addition, although nearly all specimens are fairly elongate in shape, a few are ovate.

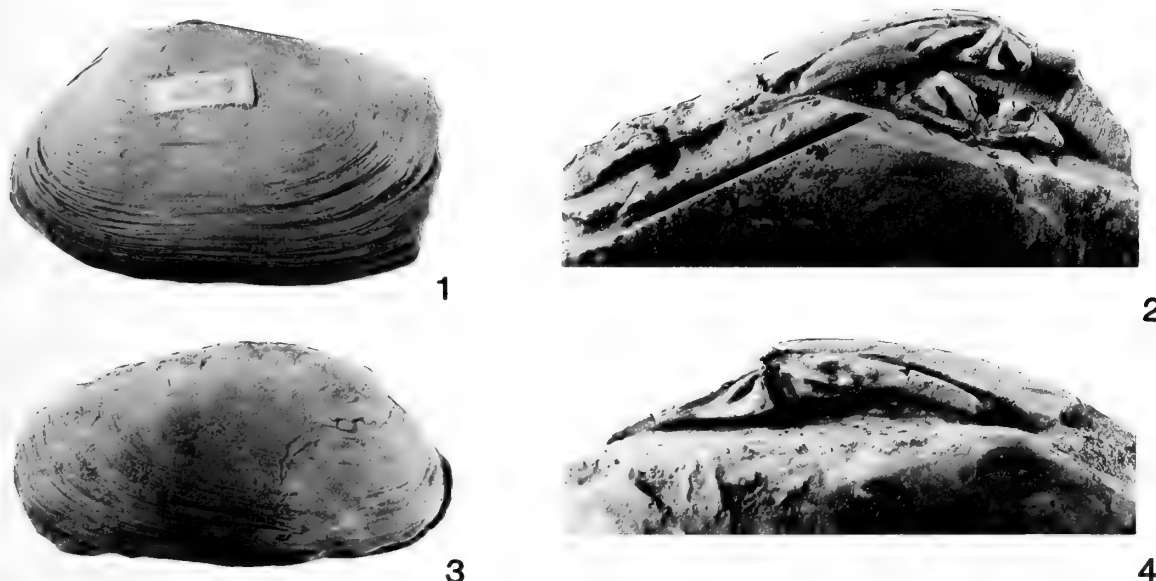
It is important to mention that the anterior cardinal of *Calyptogena* (*C.*) *gibbera* is very thin and short. To be able to recognize it in a specimen requires at least good preservation of the hinge.

Previously, *Calyptogena* (*C.*) *gibbera* was known only from its type locality at Deadmans Island (CRICKMAY, 1929a, b). Specimens were from a 12-cm-thick layer of hard gray shale that weathered to a rusty yellow. CRICKMAY (1929b) assigned this shale layer, which contained only the species *C. (C.) gibbera* and *Lucinoma acutilineata* (Conrad), to his zone No. 2. ARNOLD (1903) had included the shale in the San Diego Formation, but SMITH (1912) and CRICKMAY (1929a, b) included it in the Santa Barbara beds. CLARK (1931:37) and WOODRING *et al.* (1946), however, put CRICKMAY's (1929b) zone No. 2 in the Timms Point Silt. According to G. L. Kennedy (personal communication), the Timms Point Silt is of middle Pleistocene age.

Calyptogena (*C.*) *lasia* is known from lower Pliocene strata in southern California, predominately the Repetto Formation and, to a lesser extent, the Pico Formation of the Los Angeles basin (WOODRING, 1938) and near the top of the Towsley Formation, Ventura basin (WINTERER & DURHAM, 1962:295, pl. 46). The Towsley Formation locality is equivalent to locality LACMIP 21363.

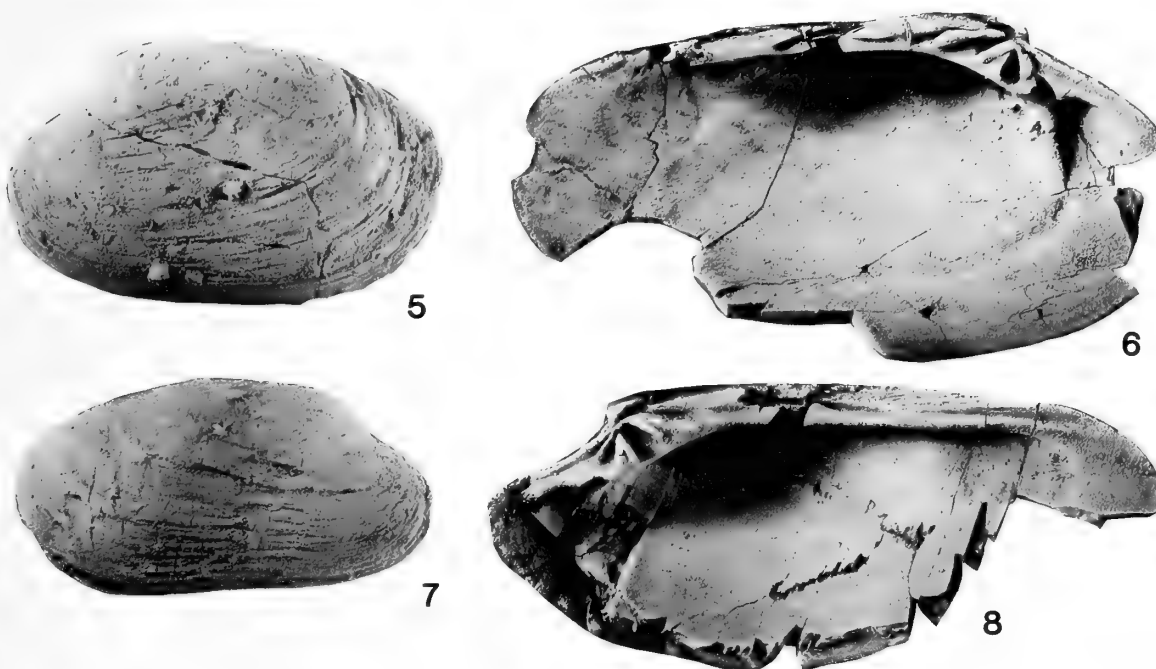
During the course of this investigation, a single specimen of a previously unidentified *Calyptogena* (*C.*) *gibbera* from locality LACMIP 11942 in the Niguel Formation, southern Los Angeles basin, also was detected. This is the first record of this genus from the Niguel Formation. According to VEDDER (1960, 1972), the Niguel Formation is of late Pliocene age.

The only other contemporaneous species of *Calyptogena*



Explanation of Figures 1 to 4

Figures 1 to 4. *Calyptogena* (*Calyptogena*) *gibbera* Crickmay, 1929, locality LACMIP 30252 = locality University of California, Los Angeles 6613. Figures 1, 2: left valves; Figure 1: hypotype and topotype, LACMIP 8398, exterior (posteriormost area missing), $\times 1.3$; Figure 2: hypotype and topotype, LACMIP 8399, hinge (anterior end of anterior cardinal is missing), $\times 1.5$. Figures 3, 4: lectotype, LACMIP 8400, right valve; Figure 3: exterior, $\times 1.1$; Figure 4: hinge, $\times 2.3$.



Explanation of Figures 5 to 8

Figures 5 to 8: *Calyptogena* (*Calyptogena*) *lasia* (Woodring, 1938). Figures 5, 6: left valves; Figure 5: hypotype, LACMIP 8401, locality LACMIP 21363, exterior, $\times 1.4$; Figure 6: holotype, USNM 496097, locality USGS 13864, hinge, $\times 2.1$. Figures 7, 8: right valves; Figure 7: hypotype, LACMIP 8402, locality LACMIP 21363, exterior, $\times 1.3$; Figure 8: holotype, USNM 496097, locality USGS 13864, hinge, $\times 2.2$.

s.s. from southern California is *C. (C.) pacifica* Dall, 1891. It has been reported from an oil-well corehole in Pliocene deposits in Beverly Hills, California (GRANT & GALE, 1931:278), and it is most commonly reported as a Recent species, known from Clarence Strait, southern Alaska, to the Santa Barbara Channel, southern California (OLDROYD, 1925; BOSS & TURNER, 1980), in depths ranging from 550 to 1950 m (BERNARD, 1983). It also has been reported from Mio-Pliocene and Pliocene deposits of Japan (OTUKA, 1937; ÔTATUME, 1942; KANNO *et al.*, 1989). As can be seen from the illustrations in WOODRING (1938: fig. 2b), in BERNARD (1974:text-fig. 2A), in BOSS (1968: figs. 16, 17, 19, 20), and in BOSS & TURNER (1980:fig. 10b, c), the dentition of *C. (C.) pacifica* is markedly different from that of *C. (C.) gibbera*. In *C. (C.) pacifica*, the anterior cardinal in both valves parallels the valve margin rather than diverging from it, and the right middle cardinal is overlapped by the anterior cardinal rather than converging with it in the direction of the beak. The shell of *C. (C.) pacifica* is also not as elongate. BERNARD (1983) reported that *C. (C.) gibbera* is the same as *C. (C.) pacifica*, but this is not the case.

During the examination of mollusks associated with specimens of *Calyptogena (C.) gibbera* from locality LAC-MIP 21363 near the top of the Towsley Formation in the Ventura basin, three adult and seven juvenile specimens *C. (C.) pacifica* were found. This is the only known record of the two species occurring together.

The only other living species of *Calyptogena* s.s. from the northeastern Pacific is *C. (C.) kilmeri* BERNARD (1974: 17–18, text-figs. 1B, 2B, 3B, 4E), known from British Columbia to northern California in depths ranging from 800 to 1200 m (BERNARD, 1983). Although BERNARD (1974) placed his species in the subgenus *Archivesica*, BOSS & TURNER (1980) placed the species in *Calyptogena* s.s. because its dentition and anatomy are so similar to those of *C. (C.) pacifica*, the type species of *Calyptogena*. *Calyptogena (C.) kilmeri* differs from *C. (C.) pacifica* and *C. (C.) gibbera* in not having a right posterior cardinal.

Occurrence: Lower Pliocene through middle Pleistocene, southern California.

ACKNOWLEDGMENTS

I am most grateful to G. L. Kennedy (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) for bringing to my attention the various lots of Pliocene and Pleistocene *Calyptogena* in the museum's collection. Without his willingness to share his knowledge of the collection, this research would not have been possible.

George L. Kennedy, F. J. Collier (National Museum of Natural History), and C. Coney (Natural History Museum of Los Angeles County, Malacology Section) arranged for loans of specimens.

The manuscript benefited from comments by Ellen J. Moore and an anonymous reviewer.

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LACMIP 11942: Elevation 236 ft, 200 m after trailers on entrance road to Marbella Country Club, San Juan Capistrano, Orange County, Southern California. Niguel Formation. Age: Late Pliocene. Collector: D. Gage, 1988.

LACMIP 21363: About elevation 1800 ft, in unsurveyed land on a knife-edge ridge between Tapo Canyon and an unnamed canyon west of Salt Canyon, 488 m (1600 ft) south and 701 m (2300 ft) east of hill 1991, north side of Santa Susana Mountains, Val Verde 7.5-minute quadrangle, 1952, Ventura County, southern California. Equivalent to WINTERER & DURHAM (1962:295, 360, and pl. 46) locality F-17. Near top of Towsley Formation. Age: Late Pliocene. Collectors: B. Kelley and J. Cooper, 1942?

LACMIP 30252: Near south end, west side of Deadmans Island, San Pedro, southern California. Locality destroyed in 1928. Lower part of Timms Point Silt. Locality = University of California, Los Angeles locality 6613. Age: Middle Pleistocene. Collector: C. H. Crickmay, probably about 1927.

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Shallow-Water Venerid Clams (Bivalvia: Veneridae) from the Pacific Coast of Colombia

by

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Abstract. During collecting trips to several localities on the Pacific coast of Colombia between 1975 and 1986, 40 species of the bivalve family Veneridae were obtained. Three species (*Pitar helenae*, *Protothaca metodon*, and *Protothaca zorritensis*) are recorded for the first time on the Colombian coast, and significant new distributional information is given for several species. Notes about habitat, bathymetric range, and geographic distribution are provided for each species.

INTRODUCTION

Veneridae bivalve species of the Pacific coast of Colombia, including Isla de Gorgona, were reported from several expeditions (*Askoy*, *Albatross*, and *Velero*) and by OLSSON (1961) and KEEN (1971), but most of these records were from moderately deep waters or from beach shells. CANTERA *et al.* (1979), PRAHL (1986), and COSEL (1986), in papers on mollusks of Isla de Gorgona, have increased the number of reported venerids. ESCALLON & CANTERA (1989) have given additional data in a paper about bivalves from Bahía Málaga. However, the shallow-water and intertidal bivalves have remained almost unknown. This paper attempts to present a complete list of venerid bivalves along the Pacific coast of Colombia, from Punta Ardita (7°28'N, 77°55'W) to Cabo Manglares (1°32'N, 79°02'W), including Isla de Gorgona (Figure 1).

THE STUDY AREA

The Pacific coast of Colombia is a tropical area with several biotopes, including sandy beaches, cliffs, rocky shores, mudflats, and mangroves. In the north, from Cabo Corrientes to Panama, there is the coastal Cordillera Baudo, which is composed of basic and ultrabasic rocks. The south is dominated by mangroves on aluvial lowlands in tidal swamps and sandy beaches in the mouths of estuaries. The climate is characterized by abundant rain (500 cm/yr) and moderate air temperatures. There is a wide tidal range (about 4 m between high and low water), currents of moderate speed, high water temperatures, and low salinities.

MATERIALS AND METHODS

During 10 years (1975-1986), several localities between Punta Ardita in the north and Cabo manglares in the south, including Isla de Gorgona, were visited in search of live and dead mollusks. Collecting was done by hand in intertidal areas, skin and SCUBA diving in shallow water, and shrimp nets in deeper water. Mollusks were fixed in 5% formalin and then transferred to 75% alcohol. They were identified in the laboratories of malacology of the Department of Biology of the University of Valle, Cali, Colombia. All material is deposited in the reference collection of Marine Biology of the University of Valle (C.R. B.M.U.V.). The habitats given here are those where the species were found in this study, and the dimensions are those of the largest specimen.

RESULTS

SYSTEMATIC ACCOUNT

Class Bivalvia
Subclass Heterodonta
Order Veneroida
Superfamily Veneroidea
Family VENERIDAE

Subfamily VENERINAE

Periglypta multicostata (Sowerby, 1835)

OLSSON, 1961:293, pl. 50, fig. 3-3b.
KEEN, 1971:161, fig. 380.

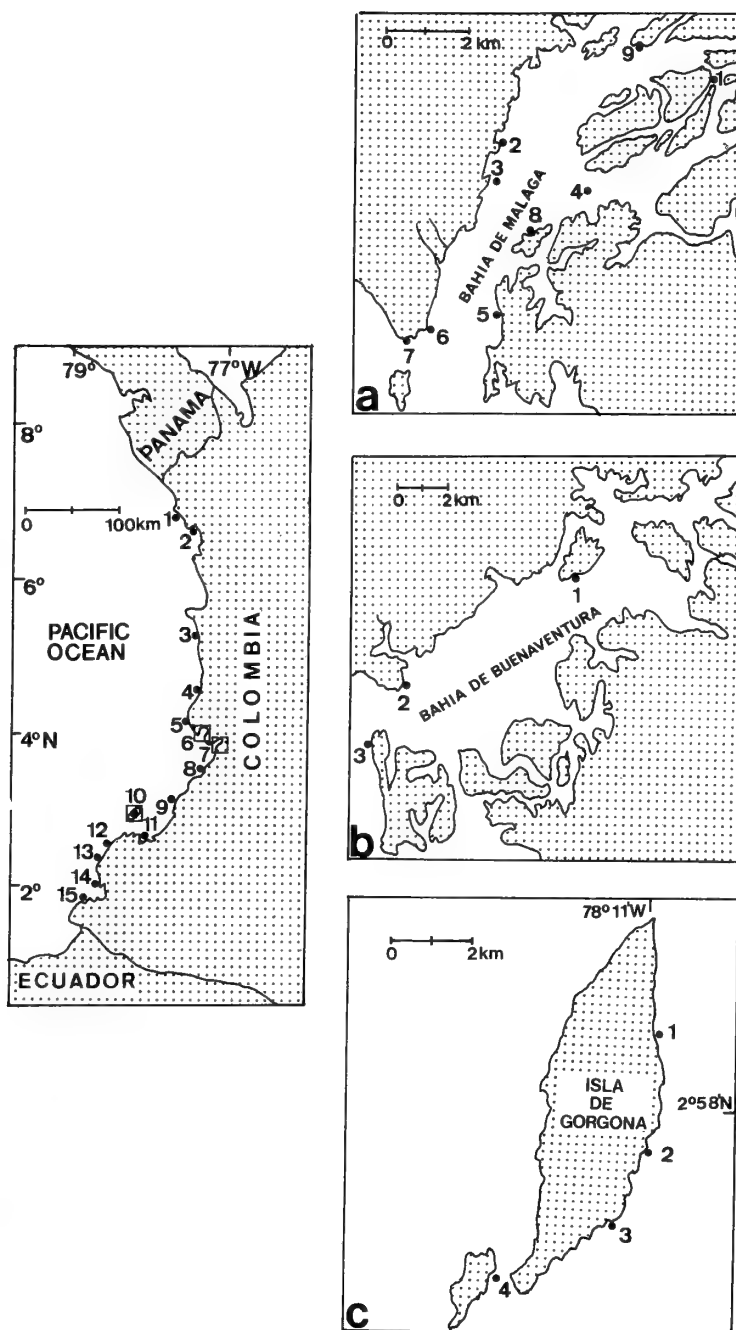


Figure 1

The Pacific coast of Colombia showing the study localities: 1. Punta Ardita; 2. Bahía Octavia; 3. Ensenada de Utria; 4. Ensenada Catripe; 5. Charambirá; 6. Bahía de Málaga (Figure 1a); 7. Bahía de Buenaventura (Figure 1b); 8. Golfo de Tortugas; 9. Punta Coco; 10. Isla de Gorgona (Figure 1c); 11. Guapi; 12. Mulatos; 13. Vigia; 14. Tumaco (Isla de Gallo); 15. Tumaco (Bocagrande).

Figure 1a. Bahía de Málaga: 1. Archipelago de la Plata; 2. Punta La Muerte; 3. Isla Curichichi; 4. Los Negros; 5. Playa Chucheros; 6. Juanchaco; 7. Ladrilleros; 8. Isla Monos; 9. Isla El Aguante.

Figure 1b. Bahía de Buenaventura: 1. Isla El Cangrejo; 2. La Bocana; 3. Punta Soldado.

Figure 1c. Isla de Gorgona: 1. Playa Pizarro; 2. Muelle; 3. Playa Blanca; 4. Gorgonilla (Estrecho de Tasca).

Material: Ensenada de Utria, Isla de Gorgona (Muelle, Playa Blanca, Gorgonilla).

Habitat: Sandy-rocky beaches at extreme low tide.

Size: 92 mm length, 88 mm height

Range: Gulf of California to Punta Verde, Perú, and Galápagos Islands.

Globivenus isocardia (Verrill, 1870)

OLSSON, 1961:292, pl. 50, fig. 2.

KEEN, 1971:162, fig. 381.

Material: Punta Ardita, Ensenada de Utria, Isla de Gorgona (Playa Pizarro).

Habitat: Mostly offshore between 20 and 80 m. Substrate unknown.

Size: 80 mm length.

Range: Gulf of California to Manta, Ecuador. KEEN (1971) gives Isla de Gorgona as the southern limit.

Subfamily MERECTRICINAE

Tivela (Pachydesma) argentina (Sowerby, 1835)

OLSSON, 1961:270, pl. 44, fig. 1.

KEEN, 1971:162, fig. 384.

Material: Ensenada de Catripe, Bahía de Málaga (Ladrilleros), Bahía de Buenaventura (La Bocana), Punta Coco, Guapi, Mulatos, Vigia, Tumaco (Isla del Gallo), Isla de Gorgona.

Habitat: Sandy beaches and bars from the intertidal zone to 25 m.

Size: 57 mm length, 46 mm height.

Range: Sonora, México, to northern Perú.

Tivela (Tivela) byronensis (Gray, 1838)

OLSSON, 1961:267, pl. 44, figs. 3, 6-8.

KEEN, 1971:162, fig. 385.

Material: Ensenada de Catripe, Bahía de Málaga (Ladrilleros). Cited by COSEL (1986) from Isla de Gorgona (Gorgonilla).

Habitat: Sandy beaches and offshore to 70 m.

Size: 29 mm length, 26 mm height.

Range: Baja California to northern Perú.

Tivela (Tivela) hindsii (Hanley, 1834)

KEEN, 1971:164, fig. 387.

Material: Ensenada de Catripe, Bahía de Málaga (Ladrilleros).

Habitat: Empty shells on sandy beaches.

Size: 35 mm length, 31 mm height.

Range: West Mexico to Ecuador.

Remarks: Some authors consider *T. hindsii* a synonym of *T. byronensis*.

Tivela (Tivela) planulata (Broderip & Sowerby, 1830)

OLSSON, 1961:269, pl. 44, fig. 5-5a.

KEEN, 1971:164, fig. 390.

Material: Ensenada de Catripe, Bahía Málaga (Ladrilleros), Guapi, Mulatos.

Habitat: Empty shells on sandy beaches.

Size: 47 mm length, 51 mm height.

Range: Baja California to Ecuador.

Subfamily PITARINAE

Pitar (Pitar) consanguineus (C. B. Adams, 1852)

OLSSON, 1961:274, pl. 45, fig. 3-3a.

KEEN, 1971:168, fig. 398.

Material: Isla de Gorgona (Playa Pizarro).

Habitat: Sandy subtidal substrate from 1 to 20 m.

Size: 25 mm length, 20 mm height.

Range: Puerto Guatulco, México, to Isla de Gorgona, Colombia (COSEL, 1986).

Pitar (Pitar) elenensis Olsson, 1961

OLSSON, 1961:275, pl. 45, fig. 1-1b.

KEEN, 1971:168, fig. 399.

Material: Golfo de Tortugas, Isla de Gorgona (Muelle, Tumaco (Isla del Gallo)).

Habitat: Sandy beach, empty shells.

Size: 27 mm length, 23 mm height.

Range: Panama to northern Perú.

Pitar (Pitar) helenae Olsson, 1961

OLSSON, 1961:276, pl. 45, fig. 2-2a.

KEEN, 1971:170, fig. 401.

Material: Isla de Gorgona (Playa Blanca).

Habitat: Sandy beach, empty shells

Size: 21 mm length, 16 mm height.

Range: Gulf of California to Panama.

Remarks: This is a new record for the molluscan fauna of Colombian Pacific. COSEL (1986) recorded this species as *P. berryi* Keen, 1971, but the specimens from Isla de Gorgona do not have the diagnostic features of this species. Instead, the shape and color match very well the description of *P. helenae* Olsson, 1961.

Pitar (Pitar) fluctuatus (Sowerby, 1851)

OLSSON, 1961:275, pl. 43, fig. 7-7a; pl. 45, figs. 5, 7.

KEEN, 1971:170, fig. 400.

Material: Isla de Gorgona (Muelle, Playa Pizarro, Playa Blanca).

Habitat: Subtidal sandy bottoms to 15 m; empty shells on intertidal sandy beaches.

Size: 62 mm length, 47 mm height.

Range: Panama to Ecuador.

Pitar (Hypanthosoma) hertleini Olsson, 1961

OLSSON, 1961:276, pl. 45, fig. 6-6a.

KEEN, 1971:170, fig. 405.

Material: Ensenada de Utria, Isla de Gorgona (Muelle, Gorgonilla).

Habitat: Sandy-coral beaches, from the intertidal zone to 2 m.

Size: 55 mm length, 44 mm height.

Range: Panama to northern Perú.

Pitar (Hysteroconcha) brevispinosus (Sowerby, 1851)

OLSSON, 1961:284, pl. 47, fig. 4-4a.

KEEN, 1971:172, fig. 407.

Material: Bahía Octavia, Ensenada Catripe, Charambirá, Bahía de Málaga (Juanchaco, Ladrilleros), Guapi, Mulatos, Vigía, Tumaco (Isla del Gallo), Isla de Gorgona (Gorgonilla).

Habitat: Empty shells on sandy beaches.

Size: 48 mm length, 38 mm height.

Range: Gulf of California to Ecuador.

Pitar (Hysteroconcha) lupanaria (Lesson, 1830)

OLSSON, 1961:283, pl. 47, fig. 1-1c.

KEEN, 1971:172, fig. 408.

Material: Ensenada de Catripe, Charambirá, Bahía de Málaga (Ladrilleros), Punta Coco, Guapi, Mulatos, Vigía, Tumaco (Bocagrande, Isla del Gallo).

Habitat: Empty shells on sandy beaches.

Size: 59 mm length, 46 mm height.

Range: Baja California to northern Perú.

Pitar (Hysteroconcha) multispinosus (Sowerby, 1851)

OLSSON, 1961:284, pl. 47, fig. 2-2d.

KEEN, 1971:172, fig. 409.

Material: Bahía de Málaga (Juanchaco, Ladrilleros), Guapi, Mulatos, Vigía, Tumaco (Isla del Gallo), Isla de Gorgona (Gorgonilla).

Habitat: Empty shells on sandy beaches.

Size: 37 mm length, 30 mm height.

Range: Gulf of California to northern Perú.

Remarks: This species has a strong resemblance to *P. lupanaria*. Specimens matching the descriptions of both species have been found on the Pacific coast of Colombia. Further work is necessary to demonstrate that these are really different species based on shell and spine sizes and general form and color.

Pitar (Hysteroconcha) roseus (Broderip & Sowerby, 1829)

OLSSON, 1961:284, pl. 47, fig. 3-3d.

KEEN, 1971:172, fig. 410.

Material: Bahía de Málaga (Ladrilleros), Mulatos, Vigía, Tumaco (Bocagrande, Isla del Gallo), Isla de Gorgona (Gorgonilla).

Habitat: On sandy bottoms, intertidal zone to 15 m; empty shells on rocky shores.

Size: 52 mm length, 40 mm height.

Range: Gulf of California to northern Perú.

Pitar (Lamelliconcha) alternatus (Broderip, 1835)

OLSSON, 1961:286, pl. 48, fig. 1-1b.

KEEN, 1971:172, fig. 411.

Material: Isla de Gorgona (Gorgonilla). Cited by OLSSON (1961) from Tumaco (Isla del Gallo) as *Lamelliconcha circinata alternatus*.

Habitat: Empty shells on a sandy coral beach.

Size: 43 mm length, 37 mm height.

Range: Gulf of California to northern Perú.

Pitar (Lamelliconcha) concinnus (Sowerby, 1835)

OLSSON, 1961:287, pl. 48, fig. 4-4c.

KEEN, 1971:174, fig. 413.

Material: Ensenada Catripe, Bahía de Málaga (Ladrilleros, Los Monos), Punta Coco, Guapi, Mulatos, Vigía.

Habitat: Empty shells on sandy beaches.

Size: 40 mm length, 31 mm height.

Range: Baja California to Paita, Perú, and Galápagos Islands (STRONG & HERTLEIN, 1939).

Pitar (Lamelliconcha) paytensis (Orbigny, 1845)

OLSSON, 1961:288, pl. 48, fig. 6-6b.

KEEN, 1971, fig. 416.

Material: Ensenada de Catripe, Guapi, Vigía, Tumaco.

Habitat: One empty shell on a sandy beach.

Size: 40 mm length, 28 mm height.

Range: Gulf of California to Perú.

Pitar (Lamelliconcha) tortuosus (Broderip, 1835)

OLSSON, 1961:288, pl. 48, fig. 5-5a.

KEEN, 1971:174, fig. 417.

Material: Ensenada de Catripe, Bahía Buenaventura (Punta Soldado), Guapi, Mulatos, Tumaco (Isla del Gallo).

Habitat: Empty shells on sandy beaches.

Size: 42 mm length, 35 mm height.

Range: Guaymas, México, to Northern Perú.

Remarks: Some authors consider it a synonym of *P. concinnus* (Sowerby, 1835).

Pitar (Lamelliconcha) unicolor (Sowerby, 1835)

OLSSON, 1961:289, p. 40, fig. 3, pl. 49, fig. 4-4a.

KEEN, 1971:174, fig. 418.

Material: Punta Ardita, Bahía Octavia, Ensenada Catripe, Bahía Málaga (Curichichi, Ladrilleros), Bahía Buenaventura (Punta Soldado).

Habitat: Empty shells from sandy beaches.

Size: 47 mm length, 39 mm height.

Range: Gulf of California to Ecuador.

Pitar (Lamelliconcha) vinaceus (Olsson, 1961)

OLSSON, 1961:287, pl. 48, fig. 2-2b.

KEEN, 1971:174, fig. 419.

Material: Bahía de Málaga (Juanchaco). Cited by OLSSON (1961) as *Lamelliconcha circinata vinacea* from Tumaco (Isla del Gallo).

Habitat: Empty shells on sandy beaches.

Size: 34 mm length, 29 mm height.

Range: México to Ecuador.

Pitar (Pitarella) catharius (Dall, 1902)

OLSSON, 1961:279, pl. 40, fig. 2; pl. 49, fig. 5-5a.

KEEN, 1971:176, fig. 421.

Material: Bahía Otavia, Ensenada Catripe, Isla de Gorgona.

Habitat: Empty shells from sandy beaches.

Size: 47 mm length, 31 mm height.

Range: Baja California to northern Perú.

Macrocallista aurantiaca (Sowerby, 1835)

OLSSON, 1961:273, pl. 46, fig. 1-1c.

KEEN, 1971:176, fig. 424.

Material: Ensenada de Utría, Bahía de Málaga (Los Negros), Isla de Gorgona (Playa Pizarro).

Habitat: Subtidal sandy bottoms, 1 to 15 m.

Size: 105 mm length, 80 mm height.

Range: Gulf of California to northern Perú and Galápagos Islands (STRONG & HERTLEIN, 1939).

Subfamily DOSINIINAE

Dosinia dunkeri (Philippi, 1844)

OLSSON, 1961:261, pl. 42, fig. 3-3b.

KEEN, 1971:178, fig. 426.

Material: Isla de Gorgona (Muelle).

Habitat: Empty shells on sandy beaches.

Size: 44 mm length, 42 mm height.

Range: Gulf of California to Zorritos, Perú, and Galápagos Islands (STRONG & HERTLEIN, 1939).

Dosinia ponderosa (Gray, 1838)

OLSSON, 1961:260, pl. 40, fig. 5; pl. 42, fig. 1-1c; pl. 43, fig. 1.

KEEN, 1971:178, fig. 427.

Material: Golfo de Tortugas, Isla de Gorgona (Gorgonilla), Tumaco (Isla del Gallo). Cited by COSEL (1986) from Isla de Gorgona (Muelle, Playa Blanca).

Habitat: Empty shells on sandy beaches.

Size: 34 mm length, 36 mm height.

Range: Gulf of California to Paita, Perú.

Subfamily CYCLININAE

Cyclinella singleyi Dall, 1902

OLSSON, 1961:265, pl. 43, fig. 5-5a.

KEEN, 1971:180, fig. 432.

Material: Tumaco (Isla del Gallo). Cited by OLSSON (1961) from the same locality.

Habitat: One empty shell on a rocky shore.

Size: 32 mm length, 29 mm height.

Range: Baja California to Perú. KEEN (1971) cited this species from Baja California to Panamá.

Subfamily CHIONINAE

Chione (Chione) subimbricata (Sowerby, 1835)

OLSSON, 1961:295, pl. 55, fig. 4-4b.

KEEN, 1971:185, fig. 443.

Material: Isla de Gorgona (Gorgonilla).

Habitat: Empty shells on sandy beaches to 9 m.

Size: 31 mm length, 32 mm height.

Range: Gulf of California to Perú.

Chione (Chionopsis) amathusia (Philippi, 1844)

OLSSON, 1961:299, pl. 41, fig. 7, pl. 51, fig. 1-1a, pl. 84, fig. 2.

KEEN, 1971:186, fig. 448.

Material: Ensenada Catripe, Bahía Málaga (Juanchaco, Ladrilleros), Bahía de Buenaventura (Punta Soldado, La Bocana), Punta Coco, Guapi, Mulatos, Vigia.

Habitat: Empty shells on sandy beaches.

Size: 35 mm length, 40 mm height.

Range: Gulf of California to Mancora, Perú.

Chione (Chionopsis) olssoni (Fischer-Piette, 1969)

KEEN, 1971:188, fig. 453.

Material: No material was examined. Cited by COSEL (1986) from Isla de Gorgona.

Habitat: One empty shell on a sandy-rocky beach (COSEL, 1986).

Size: Unknown.

Range: Isla de Gorgona to Ecuador.

Chione (Chionopsis) ornatissima (Broderip, 1835)

OLSSON, 1961:300, pl. 51, fig. 3-3a.

KEEN, 1971:188, fig. 454.

Material: Charambirá, Bahía Málaga (Ladrilleros), Bahía de Buenaventura (Punta Soldado), Guapi, Tumaco (Bocagrande).

Habitat: Empty shells on sandy beaches; live in 20-25 m on mud bottoms.

Size: 47 mm length, 45 mm height.

Range: Panama to Ecuador.

Chione (Chionopsis) pulicaria (Broderip, 1835)

OLSSON, 1961:302, pl. 52, figs. 4-4a, 5-5a.

KEEN, 1971:188, fig. 455.

Material: Isla de Gorgona. Cited from Tumaco by OLSSON (1961).

Habitat: One empty valve on a sandy beach.

Size: 11 mm length, 9 mm height.

Range: Gulf of California to Tumaco, Colombia.

Remarks: Cited by COSEL (1986) as *Chione guatulcoensis* Hertlein & Strong, 1948, but his figure suggests that it probably is *C. pulicaria*.

Chione (Iliochione) subrugosa (Wood, 1828)

OLSSON, 1961:298, pl. 51, fig. 5-5a.

KEEN, 1971:190, fig. 457.

Material: Bahía de Málaga (La Plata, Punta la Muerte, Playa Chucheros), Bahía de Buenaventura (Isla del Cangrejo), Guapi, Mulatos, Vigia, Tumaco (Isla del Gallo). Cited by COSEL (1986) from Isla de Gorgona.

Habitat: Intertidal mud flats with gravel, near to mangrove areas. Used as food in some places, mainly in Bahía Málaga.

Size: 39 mm length, 30 mm height.

Range: Gulf of California to Perú and Galápagos Islands (STRONG & HERTLEIN, 1939).

Chione (Lirophora) kellettii (Hinds, 1845)

OLSSON, 1961:296, pl. 41, fig. 5; pl. 51, fig. 4-4a.

KEEN, 1971:190, fig. 459.

Material: Isla de Gorgona.

Habitat: Muddy zones offshore in 30 m.

Size: 60 mm length, 52 mm height.

Range: Gulf of California to Perú.

Chione (Lirophora) mariae (Orbigny, 1846)

OLSSON, 1961:296, pl. 49, figs. 2, 8-8a.

KEEN, 1971:190, fig. 460.

Material: Isla de Gorgona. Cited by OLSSON (1961) from Tumaco (Isla del Gallo).

Habitat: Empty shells on sandy beaches.

Size: 20 mm length, 16 mm height.

Range: Gulf of California to Guayaquil, Ecuador.

Protothaca (Antichione) beili (Olsson, 1961)

OLSSON, 1961:310, pl. 50, figs. 1-1a, 4.

KEEN, 1971:193, fig. 465.

Material: Golfo de Tortugas, Guapi, Tumaco (Isla del Gallo).

Habitat: On intertidal muddy rocky flats.

Size: 39 mm length, 35 mm height.

Range: Panama to Ecuador.

Protothaca (Colonche) ecuadoriana (Olsson, 1961)

OLSSON, 1961:311, pl. 41, fig. 2; pl. 55, fig. 5.

KEEN, 1971:193, fig. 466.

Material: Bahía Málaga (Isla El Aguante), Tumaco (Isla del Gallo).

Habitat: Mud flats in shallow water.

Size: 38 mm length, 31 mm height.

Range: Colombia to Ecuador.

Protothaca (Leukoma) asperrima (Sowerby, 1835)

OLSSON, 1961:307, pl. 53, fig. 3-3a; pl. 54, fig. 6.

KEEN, 1971:193, fig. 467.

Material: Bahía de Málaga (La Muerte, La Plata), Bahía de Buenaventura (Punta Soldado), Guapi, Tumaco.

Habitat: In mud between the roots of mangrove trees.

Size: 42 mm length, 35 mm height.

Range: Gulf of California to Perú.

Protothaca (Leukoma) metodon (Pilsbry & Lowe, 1932)

OLSSON, 1961:308, pl. 55, fig. 3-3a.

KEEN, 1971:195, fig. 469.

Material: Bahía Málaga (La Plata), Bahía de Buenaventura (Punta Soldado), Tumaco (Bocagrande).

Habitat: Empty shells on sandy beaches.

Size: 32 mm length, 29 mm height.

Range: Guaymas, México, to Tumaco, Colombia. This is a new record for the Pacific coast of Colombia.

Protothaca (Leukoma) zorritensis (Olsson, 1961)

OLSSON, 1961:308, pl. 53, fig. 5-5a; pl. 55, fig. 6.

KEEN, 1971:195, fig. 471.

Material: Tumaco.

Habitat: Intertidal gravel-mud flats.

Size: 27 mm length, 22 mm height.

Range: Colombia (Tumaco) to Zorritos and Paita, Perú.

This is a new record for the Pacific coast of Colombia.

Protothaca (Tropithaca) grata (Say, 1831)

OLSSON, 1961:305, pl. 53, figs. 2-2b, 7.

KEEN, 1971:195, fig. 473.

Material: Bahía Málaga (Isla de Curichichi), Bahía Buenaventura (Punta Soldado).

Habitat: Mud flats near mangrove swamps.

Size: 40 mm length, 32 mm height.

Range: Gulf of California to Chile.

CONCLUSION

The shallow-water and intertidal venerid bivalves from the Pacific coast of Colombia have been poorly studied, although OLSSON (1961) and KEEN (1971) gave some data for this country. The 40 species included in this paper demonstrate that the Pacific coast of Colombia has a diverse fauna, determined mainly by the great variety of habitats, such as mud flats, mangrove swamps, rocky cliffs, rocky shores, sandy beaches, and coral reefs. Only three species cited by KEEN (1971) as occurring between a locality north of Colombia and Ecuador or Perú were not found in this study—*Cyclinella jadisi* Olsson, 1961; *Irus (Paphnotia) ellipticus* Sowerby, 1834; and *Transennella modesta* (Sowerby, 1835).

The greatest number of species found on the Pacific coast of Colombia were associated with soft bottoms, mainly sandy beaches and mud flats. Most species were collected as empty shells on sandy beaches (55.0%). Most of the species collected alive are associated with sandy subtidal bottoms (17.5%) and muddy substrates in or near mangrove swamps (12.5%). The other two abundant substrates have three species (7.5%) each.

The venerids of the Pacific coast of Colombia are mainly characteristic of the Panamic Province, having a geographic distribution between the southern Gulf of California (64.8%) and northern Peru (57.8%). México is the northern limit for 80% of species and Panama is for 10.8%;

26.2% of species have Ecuador as a southern limit. Four taxa—*Pitar consanguineus*, *Pitar elenae*, *Chione pulicaria*, and *Protothaca metodon*—have a Colombian locality as a southern limit, and three—*Chione olssoni*, *Protothaca ecuadoriana*, and *Protothaca zorritiensis*—have Colombia as a northern limit.

Only one species, *Protothaca grata*, reaches Chile. In spite of relatively abundant malacological fauna of the Indo-West Pacific (EMERSON, 1967, 1978), no venerid from this area was found on the Pacific coast of Colombia. Only few species of this family inhabit coral environments, the main biotope of Central Pacific islands, and there are no records of long-survival veliger (teleplanic) larvae in this family that could facilitate their reaching different islands of the Central Pacific Ocean (SCHELTEMA, 1986). The alternative modes of long distance dispersal—adult migration, transport by rafting, and human activities—are not possible because of the particular life conditions of Veneridae and the areas that they inhabit (sandy and muddy beaches).

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First Record of the Indo-Pacific Gastropod *Cypraea caputserpentis* (Linnaeus, 1758) at Isla de Gorgona, Colombia

by

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Abstract. The present paper records an extension of the known geographical range for *Cypraea* (*Erosaria*) *caputserpentis*. This species is of wide western Indo-Pacific distribution in eastern and southern Africa, eastern and southern Asia, Australia, the islands of Polynesia, and Hawaii. The only previous records in the eastern Pacific are from Clipperton Island and Cocos Island. The new record is based on a single empty shell collected in November 1988 at Isla de Gorgona, 30 km off the mainland of Colombia and about 2300 km southeast of Clipperton Island.

INTRODUCTION

Several Indo-Pacific species of mollusks, mainly gastropods of the families Architectonicidae (ROBERTSON, 1976, 1980), Conidae (EMERSON, 1978), Coralliophilidae (EMERSON, 1978; CANTERA *et al.*, 1979), Mitridae (COSEL, 1977) and Cypraeidae, have been recorded from the eastern Pacific.

The most commonly reported Indo-Pacific cypraeid in eastern Pacific waters is *Cypraea teres* Gmelin, 1791, which has been found at Clipperton Island (HERTLEIN & EMERSON, 1953; HERTLEIN & ALLISON, 1960; EMERSON, 1967); the Galápagos Islands (EMERSON & OLD, 1965, 1968), Bahía Honda, Panama (BAKUS, 1968), Isla Malpelo (BIRKELAND *et al.*, 1975) and Isla de Gorgona (COSEL, 1986; CANTERA, 1986). BURGESS (1985) considers some of the citations of *C. teres* in the eastern Pacific to be referable to *C. alisonae* Burgess, 1983. *Cypraea talpa* Linnaeus, 1758, has been recorded from Cocos Island (SHASKY, 1983) and western Panama (EMERSON, 1983). The other species in the eastern Pacific area are cited by KEEN (1971): *Cypraea depressa* Gray, 1824; *C. maculifera* Schilder, 1932; *C. scurra indica* Gmelin, 1791; *C. helvola* Linnaeus, 1758; *C. schildersorum* (Iredale, 1939); *C. vitellus* Linnaeus, 1758; and *C. moneta* Linnaeus, 1758. All of these species are found on Clipperton Island.

Cypraea moneta is also known from the Galápagos Islands (HERTLEIN, 1937; FINET, 1987) and Cocos Island (MONTROYA, 1983). *Cypraea rashleighana* Melvill, 1888, has been recorded only from Cocos Island (CATE, 1969) but SHASKY (1989) considers it as *C. alisonae* Burgess,

1983. *Cypraea caputserpentis* was recorded previously from Clipperton Island (HERTLEIN & ALLISON, 1960) and Cocos Island (SHASKY, 1989). The present paper records an empty shell of the latter species from a sandy gravel beach on Isla de Gorgona, Colombian Pacific, the first record of this taxon from West American borderland.

Gorgona (2°58'N, 78°11'W), a volcanic island located 30 km from the Pacific coast of Colombia, was attached to the continent by the Baudó "cordillera" which was submerged in the Miocene (HAFFER, 1970). The coast of Gorgona has rocky cliffs, rocky shores, and sandy beaches, and in some regions there are coral reefs of irregular sizes in shallow water to 15 m depth. Southward is Gorgonilla, a smaller island separated from Gorgona by the 700-m wide Tasca Strait.

THE SPECIMEN FROM GORGONA

Description

The only specimen of *Cypraea caputserpentis* from Gorgona (Figure 1) does not differ significantly from the specimen illustrated by BURGESS (1985). The specimen from Gorgona has 14 teeth on the inner lip and 16 on the outer lip. The color is typical of this species: a background of chocolate brown on the marginal zones, and spots varying in size and form, forming a reticulate pattern, on the central zone. The base is chocolate brown on the periphery, with white or creamy callus near the aperture. The region of teeth is white separated by interspaces of chocolate brown. The shell interior is brown. The dimensions are 33 mm

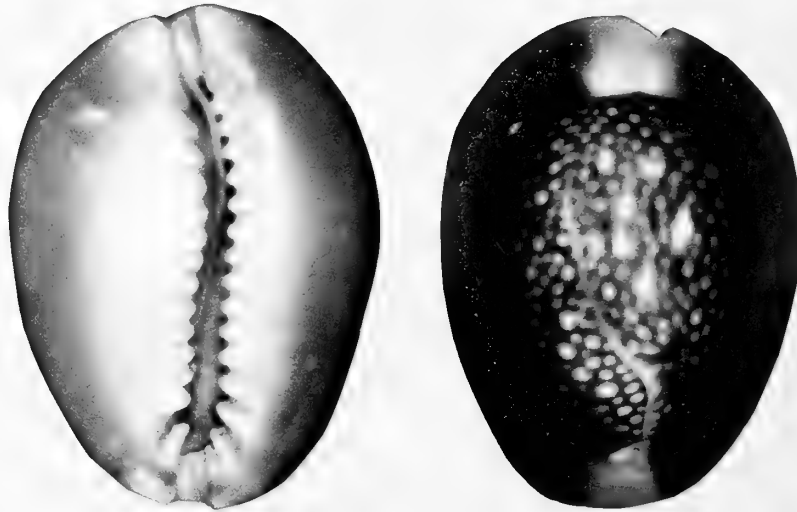


Figure 1

Cypraea (Erosaria) caputserpentis (Linnaeus, 1758) collected at Isla de Gorgona (length, 33 mm; width, 24.5 mm; height, 22 mm).

length, 24.5 mm width, and 22 mm height. The specimen is deposited in the malacological collection of the University of Valle, Cali, Colombia (No. 88098).

Habitat

This record is based on a dead, but well preserved shell collected at 2-m depth between the islands of Gorgona and Gorgonilla on sandy gravel, near coral colonies in November 1988. The principal corals in the zone are species of *Pocillopora*, *Pavona*, and *Porites*.

Geographic Distribution

The species *Cypraea caputserpentis* has a wide distribution in the Indo-Pacific and in some localities of the eastern Pacific (BURGESS, 1985). Furthermore some records of this species by HIDALGO (1906) were not cited by BURGESS (1985): southern Africa (El Cabo, Natal); eastern Africa (Reunion, Almirantes, Seychelles, Egypt); southern Asia (Laccadives, India, Andaman, Nicobar, Malacca); and eastern Asia (Hainan, Taiwan, China, Marianas, Carolinas). The previous nearest records to Isla de Gorgona are of HERTLEIN & ALLISON (1960), who recorded *C. caputserpentis* from Clipperton Island, and of SHASKY (1989) who recorded it from Cocos Island.

DISCUSSION AND CONCLUSIONS

Although based on a single shell, this paper presents a new record of *Cypraea caputserpentis* from the eastern Pacific, confirming earlier records of this species from Clipperton Island and Cocos Island. However, little is known about the possible establishment of viable populations of *C. caputserpentis* in the eastern Pacific, and it is possible that the shell found at Gorgona was transported as a veliger from Polynesia, from other islands of the central Pacific, or from an established population on eastern Pacific islands (Cocos and Clipperton). These islands could serve as "migratory bridges" for some Indo-Pacific species that have teleplanic larvae, as is suggested by SCHELTEMA (1986) for other families of prosobranch gastropods such as Architectonicidae, Cymatiidae, Bursidae, and Coralliophilidae.

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A New Epitoniid Species from the Pacific Coast of the Kii Peninsula, Japan

by

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Abstract. *Graciliscala koshimagani* sp. nov. is described. It is parasitic on an undetermined *Epizoanthus* species, which occurs on the carapace of the crab *Leotomithrax edwardsi* (de Haan, 1839). The new species appears to be morphologically close to *Graciliscala ishimotoi* Masahito & Habe, 1976, or *Graciliscala rimbogai* Masahito & Habe, 1976, but differs in having a more inflated body whorl and more axial costae.

INTRODUCTION

Several minute epitoniids were collected in 1988 from an undetermined species of *Epizoanthus* attached to the carapace of the crab *Leotomithrax edwardsi* (de Haan, 1839). The crabs were gathered with a lobster gill net set on the seabed off Kirimezaki, Kii Peninsula, Wakayama Japan. These epitoniids are classified in the genus *Graciliscala* by their conchological characters (REEVE, 1874; DE BOURY, 1909). MASAHITO & HABE (1976) reported two *Graciliscala* species collected from the same region, off Kii Peninsula, Japan. Furthermore, according to their description, these two *Graciliscala* species are also parasitic on minute sea anemones of the genus *Epizoanthus*. However, conchological characters indicate that the specimens collected in 1988 represent a new species of the genus *Graciliscala*.

TAXONOMY

Family Epitoniidae Röding, 1798

Genus *Graciliscala* de Boury, 1909

Graciliscala koshimagani Nakayama, sp. nov.

(Figures 1-6, 10)

Description: Shell rather small, thin, milky white, pyramidally ovate, becoming attenuate toward the small apex. Spire elevated pyramidally with 8 or 9 whorls. Surface with 12 or 13 thin axial costae, interspaces between each two costae crossed by 20-25 very fine spiral threads. Protoconch of 4 smooth, polished whorls. Teleoconch whorls 4 or 5 in number, well rounded with deep suture and slightly separated by riblets. Body whorl width about one-half of shell height and well rounded at the periphery. Aperture ovate, but not angular, rounded, thickened and reflexed at the last costa. Umbilicus closed. Operculum ovate, thin light yellowish brown and paucispiral.

Type deposition and measurements: Type specimens are deposited in the University of California Museum of Paleontology. Holotype, height 5.0 mm and width 3.0 mm (UCMP Type No. 38641); paratype 1, height 6.0 mm and width 3.2 mm (UCMP Type No. 38642); paratype 2, height 3.5 mm and width 2.1 mm (UCMP Type No. 38643).

Explanation of Figures 1 to 9

Figures 1 and 2. *Graciliscala koshimagani* sp. nov., holotype, off Kii Peninsula, Japan, 34°00'N, 134°48'E, 90 m deep (UCMP 38641), 5.0 mm.

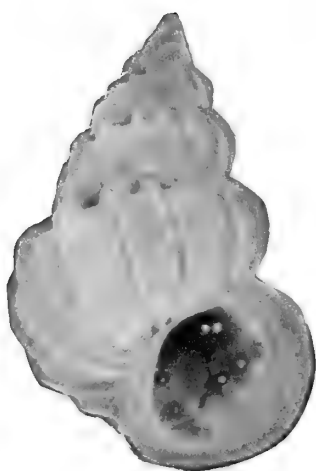
Figures 3-5. *Graciliscala koshimagani*, paratype 2 (UCMP 38643), 3.5 mm.

Figure 6. Electron micrographs of protoconch of *Graciliscala koshimagani*, scale line = 64.5 μ m.

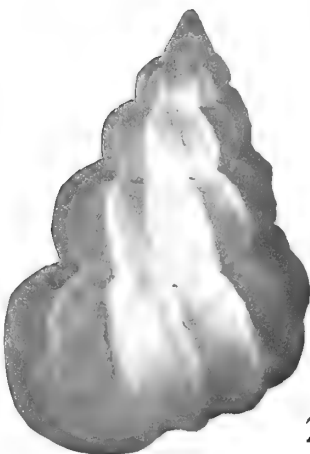
Figures 7 and 8. *Graciliscala rimbogai* Masahito & Habe, 1976, off Kii Peninsula, Japan, 7.0 mm.

Figure 9. Electron micrograph of protoconch of *Graciliscala rimbogai*, scale line = 106 μ m.

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1



2



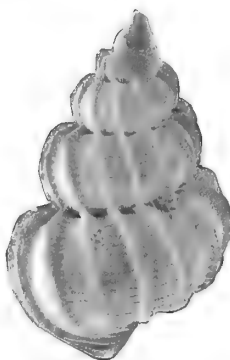
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3



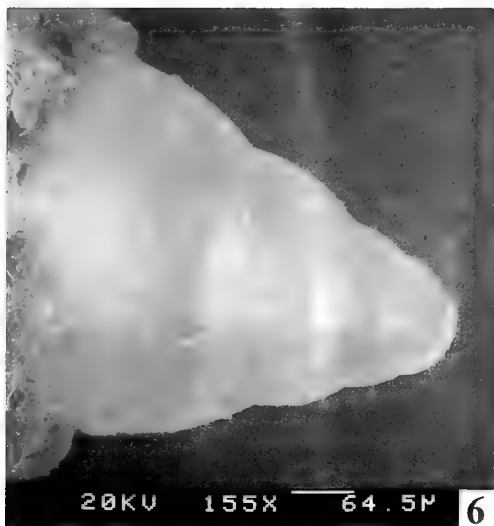
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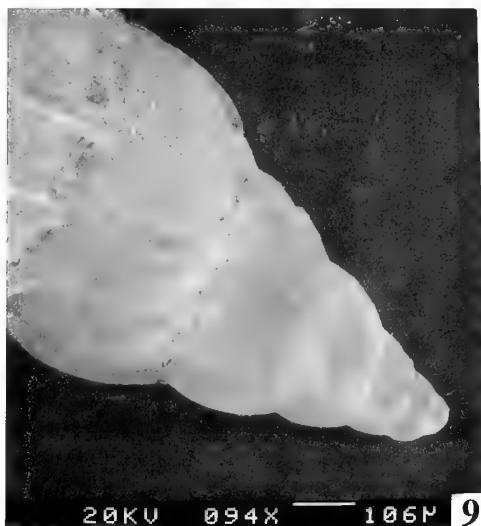
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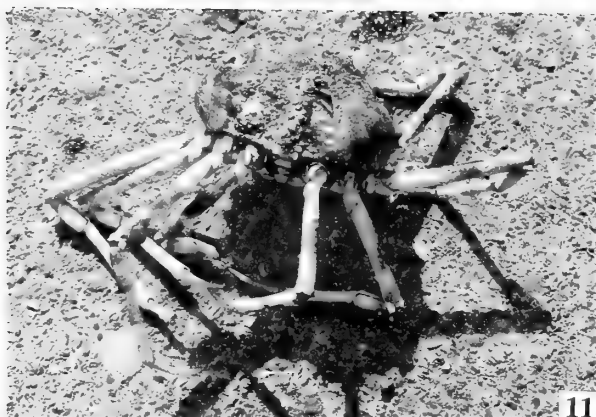
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9



10



11

Explanation of Figures 10 and 11

Figure 10. *Graciliscala koshimagani*, parasitic on the cnidarian *Epizoanthus* sp. attached to the carapace of the crab *Leotomithrax edwardsi*.

Figure 11. *Leotomithrax edwardsi* (de Haan, 1839), host of the *Epizoanthus* sp., 30 cm.

Type locality: Offshore Kirimezaki, Kii Peninsula, Minabe Wakayama, Japan (34°00'N, 134°48'E) about 90–120 m deep.

Etymology: *koshimagani* is derived from the Japanese name for *Leotomithrax edwardsi*.

REMARKS

This new species is parasitic on an undetermined species of *Epizoanthus* attached to the carapace of the crab *Leotomithrax edwardsi* (de Haan, 1839). UTSUMI (1976) showed that some *Actiniaria* species also occur on *L. edwardsi*, but this new species is not associated with *Actiniaria*. Although *Leotomithrax edwardsi* may have several tiny zoanthids on its carapace, the new species is found only on the *Epizoanthus* species (Figures 3, 10).

From a conchological point of view, this new species is similar to *Graciliscala rimbogai* Masahito & Habe, 1976, but differs by having a more inflated body whorl. The shell height–width ratio of the new species is 1.5–1.9, while in *G. rimbogai* it is 2.2–2.5. Moreover, the new species has 12 or 13 costae where *G. rimbogai* has only 10 or 11. The new species also resembles *Graciliscala ishimotoi* Masahito & Habe, 1976, but *G. koshimagani* sp. nov. can be easily distinguished by its thin costae and pyramidal shape.

Most species of *Graciliscala* occur on species of *Epizoanthus* but the primary associations of *G. koshimagani* sp. nov. differ from those of other *Graciliscala* species. *Graciliscala ishimotoi* is parasitic on *Epizoanthus ramosus* Cargren, which is attached to the surface of dead gastropods such as *Pterynotus pinnatus* (Wood, 1815); *G. rimbogai* is parasitic on an undetermined species of *Epizoanthus* attached to the surface of *Guildfordia triumphans* Philippi, 1841.

ACKNOWLEDGMENTS

I am very grateful to Messers Torao Yamamoto and Manabi Manabe who gave me a chance to write this paper. Also I have to note special thanks to Messers Hirokuni Noda and Kouichi Takenouchi who took the photos used in Figures 10 and 11, respectively. I also thank Dr. David Lindberg who was kind enough to review an early draft of this manuscript.

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NOTES, INFORMATION & NEWS

Possible Antagonistic Behavior by
Pteraeolidia ianthina
(Nudibranchia: Aeolidioidea)

by

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In *The Veliger* of 3 April 1989, Dr. Richard Willan reported that he had witnessed antagonistic behavior by *Pteraeolidia ianthina* (Angas) (WILLAN, 1989). On 28 January 1990, we witnessed a similar type of behavior whilst diving at a depth of 12 m at the diving location known as Coral Grotto off Heron Reef in Queensland, Australia. We observed three adult (approximately 50 mm extended crawling length) *Pteraeolidia ianthina*. Two were passive but the third animal was continually flailing the anterior half of its body towards one of the other animals. On closer observation this behavior seemed to be triggered when the agitated animal came in contact with a mucous trail left by one of the other animals. This mucous trail was distinctive in that grains of sand were stuck to it. The passive animal continued to move slowly in one direction during the encounter and showed no response to the activity of the other. Although each lunge brought the active *Pteraeolidia* close to the passive animal, as far as we could see they at no time made actual contact. The third *Pteraeolidia* did not move throughout the encounter. After about five minutes the active *Pteraeolidia* moved away and neither of the other animals tried to follow it.

This behavior might not necessarily be antagonistic. LONGLEY & LONGLEY (1981) described similar behavior in *Hermisenda crassicornis* but as a preliminary to mating. We may have observed a situation in which one animal was prepared to mate but the other animal was uninterested. A response to mucous trails is not unknown to opisthobranch mollusks: the cephalaspidean *Navanax inermis* detects prey by mucous trail contact (PAINE, 1963) and also responds to alarm pheromones in mucous trails of the same species (SLEEPER *et al.*, 1980).

We should like to thank Robert Burn for his comments and for drawing our attention to the paper by Longley and Longley.

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Notes on the Distribution, Taxonomy, and
Natural History of Some North Pacific Chitons
(Mollusca: Polyplacophora)

by

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During the past seven years of investigations of the chiton fauna of the North Pacific, several distribution records have been noted. These records are reported here along with taxonomic and ecological notes.

Voucher specimens for most of the distribution records have been deposited in the Los Angeles County Museum of Natural History (LACM). Other voucher specimens are in the Royal British Columbia Museum (RBCM), Victoria, British Columbia, Canada, and the California Academy of Sciences (CAS), San Francisco, California.

Other abbreviations used in the text are as follows: United States National Museum of Natural History (USNM) Washington, D.C.; Santa Barbara Museum of Natural History (SBMNH), Santa Barbara, California; Zoological Institute Academy of Sciences (ZIAS), Leningrad, USSR; and the private collection of the author (RNC).

LEPIDOPLEURIDAE

Hanleyella asiatica Sirenko, 1973

Previous known distribution: Bering Sea (Providence Bay and Anadyr Bay, NE Siberia) to the Kurile Islands (Paramushir, Onkotan, Simoshir, and Urup islands), USSR (SIRENKO, 1973), 10-130 m on rocks.

New records: Six specimens (RNC), 3.5-6.0 mm long, Bering Sea, N of Umnak Island, Aleutian Islands, Alaska (52°50.71'N, 168°22.56'W), 198-258 m, on cobbles. Collected by RNC, 3 June 1985.

Four specimens (one LACM 141148), 5.0-5.5 mm long, Gulf of Alaska, W of Dall Island, extreme SE Alaska (55°00.01'N, 133°57.47'W), 252 m on mud/gravel bottom. Collected by Rae Baxter, 28 August 1987.

Remarks: In the Aleutians, *Hanleyella asiatica* was taken

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on large cobbles along with *Leptochiton alveolus* (Loven, 1846) and *Placiphorella pacifica* Berry, 1919.

The new records extend the known range about 4000 km to the east.

LEPIDOCHITONIDAE

Lepidochitona berryana Eernisse, 1986

Previous known distribution: Pigeon Point, San Mateo County, California, to Palos Verdes, Los Angeles County, California (EERNISSE, 1986), intertidal and shallow subtidal.

New records: Thirty-two specimens (LACM 66-2), 5.0–21.5 mm long, Camalu, Baja California Norte, Mexico (30°50'N, 116°5'W), intertidal on rock ledges and boulders. Collected by James H. McLean and P. Oringer, 5–6 January 1966.

Seven specimens (RNC), 12.0–16.5 mm long, Punta Banda, Baja California Norte, Mexico (31°34'N, 116°40'W), intertidal on rocks. Collected by RNC, A. Todd Moore, and David Forrester, 26 January 1982.

One specimen (LACM 68-12), 6.0 mm long, Bahía Guasimas, near Guaymas, Sonora, Mexico (27°59'N, 110°54'W), 25 m on rock. Collected by James H. McLean. *Remarks:* The new records extend the known range about 440 km to the south on the Pacific coast, and into the Gulf of California.

Tonicella insignis (Reeve, 1847)

Previous known distribution: Dutch Harbor, Unalaska Island, Aleutian Islands, Alaska (BAXTER, 1987) to Washington State (RICE, 1972), intertidal to 52 m.

New records: One specimen (RNC), 22.0 mm long, Simpsons Reef, off Cape Arago, Coos County, Oregon (43°18.30'N, 124°25.30'W), 30 m on rock face. Collected by RNC, 7 July 1984.

Two specimens (one LACM 141152) 6.7 and 17.0 mm long, Orford Reef, Curry County, Oregon (42°46'N, 124°36'W), 20 m on rock ledge. Collected by RNC, 11 March 1984.

Four specimens (RNC) 18–26 mm long, Blanco Reef, Curry County, Oregon (42°50'N, 124°35'W), 30–34 m on rock ledges and cobbles. Collected by RNC, 15 March 1989.

Remarks: Specimens from Blanco Reef were taken along with other, somewhat scarce chitons, *Mopalia phorminx* Berry, 1919, and *Lepidozona scabricostata* (Carpenter, 1864).

The new records extend the known range 650 km to the south.

Dendrochiton semilirata Berry, 1927

Previous known distribution: Departure Bay, Vancouver Island, British Columbia, Canada to Pyramid Cove, San Clemente Island, California (FERREIRA, 1982), 38–141 m.

New record: Forty-three specimens (five of them LACM

144619), 3.0–10.0 mm long, off Inlet Point, Port Chester (Metlakatla), Annette Island, SE Alaska (55°09'N, 131°33'W), at 42 m on clean (*i.e.*, free of silt or mud) gravel. Collected by RNC, 25 August and 3 September 1990.

Remarks: An examination of the data of all other known specimens of *Dendrochiton semilirata* indicates that this species seems to prefer the clean gravel habitat.

The new record extends the known range 690 km to the north.

Juvenichiton albocinnamomeus Sirenko, 1975

Previous known distribution: Kurile Islands (Paramushir Island to Iturup Island) to Commander Islands, USSR (SIRENKO, 1975b), intertidal to 45 m on the alga *Thalassiophyllum clathrum*.

New records: One hundred and three specimens (five LACM 141150), 1.5–8.0 mm long, Ram's Head Point, near entrance to Chernofski Harbor, NW end of Unalaska Island, Aleutian Islands, Alaska (53°24'N, 167°32'W), intertidal on *Thalassiophyllum clathrum*. Collected by RNC and David Forrester, 1–2 April 1985.

Forty-seven specimens (RNC), 2.0–8.0 mm long, Korovin Bay, Atka Island, Aleutian Islands, Alaska (52°14'N, 174°18'W), intertidal to 6 m on *Thalassiophyllum clathrum*. Collected by RNC, 21 August 1985.

Remarks: KAAS & VAN BELLE (1985) placed this species in the synonymy of *Juvenichiton saccharinus* (Dall, 1878) on the basis of the examination of a paralectotype of *Tonicella saccharina* Dall (USNM 30912) from Kiska Island, Aleutian Islands, in comparison with topotypes of *J. albocinnamomeus* from Onkotan Island, Kurile Islands. However, I believe this synonymy to be an error.

Juvenichiton albocinnamomeus is a valid species, and *Juvenichiton kommandorensis* Sirenko, 1975 (described as endemic to the Commander Islands) is a synonym of *J. saccharinus*. The original syntype series of *Tonicella saccharina* was from various localities in the Shumagin and Aleutian Islands, and may have included specimens of both of these similar species. FERREIRA (1982) designated the syntype series as lectotype (USNM 30914, larger specimen) and paralectotypes (USNM 30914, smaller specimen, USNM 30913, USNM 30912, and USNM 30911). Another specimen from the original syntype series is in the S. S. Berry collection (SBMNH 34457). The Berry specimen is from the type locality—Yukon Harbor, Big Koniui Island, Shumagin Islands—and bears the same data as the lectotype. A comparison of the Berry specimen, along with photographs of the lectotype (through the kindness of the late Dr. Antonio J. Ferreira), five topotypes of *J. kommandorensis* (through the kindness of Dr. B. I. Sirenko, ZIAS) and two specimens from Ram's Head Point, near the entrance to Chernofski Harbor, Unalaska Island, Aleutian Islands (RNC, 1 April 1985, 12 m on the alga *Constantinea subulifera*), with three topotypes of *J. albocinnamomeus* (also from Sirenko) and the more than one

hundred specimens from the Aleutians revealed the error. I believe that the paralectotype of *T. saccharina* designated by KAAS & VAN BELLE (1985) is a specimen of *J. albocinnamomeus*, but the lectotype and the Berry specimen are identical to the topotypes of *J. kommandorensis*. Thus I recommend that *J. kommandorensis* be treated as a synonym of *J. saccharinus*, and *J. albocinnamomeus* be reinstated as a valid species.

Juvenichiton albocinnamomeus is found exclusively on the alga *Thalassiophyllum clathrum*, from the intertidal to a depth of about 45 m. At depths of 10–45 m, *J. saccharinus* lives only on the alga *Constantinea subulifera*.

Juvenichiton albocinnamomeus may be distinguished from *J. saccharina* by the color of the valves; *J. saccharinus* has red central areas and white lateral areas whereas *J. albocinnamomeus* is overall cream to tan, usually with reddish-brown jugal triangles, although some specimens are solid cream colored.

The new records extend the known range about 1200 km to the east.

Juvenichiton deplanatus Sirenko, 1975

Previous known distribution: Northern Kurile Islands (Paramushir Island and Makanrushi Island) to Commander Islands, USSR (SIRENKO, 1975b), intertidal to 10 m on rocks.

New record: Three specimens (one LACM 141158), 1.5–3.0 mm long, Nazan Bay, Atka Island, Aleutian Islands, Alaska (52°12'N, 174°11'W), 5–6 m on rocks. Collected by RNC, 22 August 1985.

Remarks: *Juvenichiton deplanatus* may be distinguished from *Micichiton grandispina* and *Spongioradsia aleutica* by the lack of large, ribbed or striated scales on the girdle and by the shape of the valves. *Juvenichiton deplanatus*, like *M. grandispina* has 11 teeth per transverse row of the radula.

The new record extends the known range about 1200 km to the east.

Micichiton grandispina Sirenko, 1975

Previous known distribution: Kurile Islands (Paramushir Island to Urup Island) to Commander Islands (SIRENKO, 1975b), 0–50 m.

New record: Two specimens (one LACM 141151), 2.0 and 4.0 mm long, Korovin Bay, Atka Island, Aleutian Islands, Alaska (52°14'N, 174°18'W), intertidal on rocks. Collected by RNC, 21 August 1985.

Remarks: This small species may be distinguished from the very similar appearing *Spongioradsia aleutica*, with which it shares the same habitat, by the stronger sculpture on the lateral areas, the unslitted intermediate valves, and the radula, which has only 11 teeth per transverse row instead of the normal 17.

The new record extends the known range 1200 km to the east.

ISCHNOCHITONIDAE

Lepidozона cooperi (Carpenter MS, Dall, 1879)

Previous known distribution: Neah Bay, Clallum County, Washington State (RICE, 1972) to Punta Santo Tomas, Baja California Norte, Mexico (FERREIRA, 1978), intertidal to 20 m.

New record: Two specimens (one LACM 141161), 33.0 and 34.5 mm long, S side of Quisitus Point, Florencia Bay, SW Vancouver Island, British Columbia, Canada (49°00'N, 125°40'W), intertidal on bottoms of rocks. Collected by Graham and Sue Jeffrey, 2 July 1986.

Remarks: The new record extends the known range about 62 km to the north.

Lepidozона scabricostata (Carpenter, 1864)

Previous known distribution: Cape Flattery, Clallum County, Washington (FERREIRA, 1978) to Sebastian Vizcaino Bay, Baja California Norte, Mexico (FERREIRA, 1978), intertidal (extremely rare) and 30–1460 m on rocks and sand.

New records: One specimen (RBCM, Cowan Collection No. 6760), 14 mm long, off Biorka Island, Sitka Sound, Baranof Island, Alaska (42°04'N, 124°17'W), 201–208 m.

One specimen (RNC) 6.0 mm long, Gulf of Alaska, W of Icy Point, SE Alaska (58°35.03'N, 138°27.25'W), 190 m. Collected by Rae Baxter, 16 August 1987.

Three specimens (one LACM 141149), 5.5–6.0 mm long, Gulf of Alaska, SW of Lituya Bay (Glacier Bay National Monument) (57°50.12'N, 136°48.71'W), 119 m. Collected by Rae Baxter, 12 August 1987.

Remarks: The new records extend the known range 1175 km to the north.

Lepidozона (Tripoplax) ima Sirenko, 1975

Previous known distribution: NW Pacific Ocean, near Commander Islands, USSR (SIRENKO, 1975a) and off Baranof Island, SE Alaska (KAAS & VAN BELLE, 1987), 100–1180 m.

New records: One specimen (RNC), 16.0 mm long, Bering Sea, N of Umnak Island, Aleutian Islands, Alaska (52°50.71'N, 168°22.56'W), 228–274 m on small boulder. Collected by RNC, 2 June 1985.

Four specimens (one LACM 141154), 18.0–25.0 mm long, S of Rat Island, Aleutian Islands, Alaska (51°53.34'N, 179°45.58'E), 121 m on rocks. Collected by Rae Baxter, 7 September 1986.

Remarks: This is the first record of *Lepidozона ima* in the Aleutians, and bridges the gap in its previous known distribution.

Lepidozона (Tripoplax) regularis (Carpenter, 1855)

Previous known distribution: Crescent City, Del Norte County, California (CHACE & CHACE, 1933) to San Diego,

San Diego County, California (KAAS & VAN BELLE, 1987), intertidal to 15 m.

New records: Five specimens (one LACM 141153), 19.0–33.5 mm long, S end of Harris Beach, Brookings, Curry County, Oregon (42°05'N, 124°17'W), 1–1.5 m on bottoms of large rocks. Collected by RNC, 28 July 1982.

Seven specimens (RNC), 22.5–37.0 mm long, N of Zwagg Rock, Mill Beach, Brookings, Curry County, Oregon (42°04'N, 124°17'W), 1–5 m on bottoms of large smooth rocks. Collected by RNC and Dan Kerns, 27 August 1984.

Remarks: The new records extend the known range 37 km to the north.

Lepidozona (Tripoplax) trifida
(Carpenter, 1864)

Previous known distribution: Shumagin Islands, Alaska, to Puget Sound, Washington State (BURGHARDT & BURGHARDT, 1969), intertidal to 110 m on rocks.

New record: One specimen (LACM 141157), 19.0 mm long, Dutch Harbor, Unalaska Island, Aleutian Islands, Alaska (55°54'N, 166°31'W), 7 m on rock. Collected by Rae Baxter, 22 September 1986.

Remarks: A wolf-eel (*Annarhichthys ocellatus*) taken at 82 m, NE of Middleton Island, Gulf of Alaska (*leg.* Rae Baxter, 16 July 1989) contained the partially digested remains of three adult specimens (two LACM 141169) of *Lepidozona trifida* in its stomach, indicating that this chiton is actively preyed upon.

The new record extends the known range about 385 km to the west.

Stenosemus stearnsii (Dall, 1902)

Previous known distribution: Trinidad, Humboldt County, California (TALMADGE, 1973) to Santa Clemente Island, San Diego, California (FERREIRA, 1978), 439–648 m.

New record: One specimen (CAS 012626), 14.0 mm long, SW of Seaside, Clatsop County, Oregon (45°50'N, 124°43.03'W), 400 m.

Remarks: The new record extends the known range 650 km to the north.

MOPALIIDAE

Mopalia imporata (Carpenter, 1864)

Previous known distribution: Kachemak Bay, Kenai Peninsula, Cook Inlet, Alaska (CLARK, 1983, as *Mopalia cithara* Berry, 1951) to La Jolla, San Diego County, California (BURGHARDT & BURGHARDT, 1969), intertidal to 120 m.

New record: Four specimens (one LACM 141165), 8.0–23.5 mm long, Punta Santo Tomas, Baja California Norte, Mexico (31°34'N, 116°40'W), intertidal to 3 m on bottoms of rocks. Collected by RNC and David Forrester, 26 January 1982.

Remarks: A comparison of the holotype of *Mopalia cithara*

Berry, 1951 (SBMNH 34422) with over 50 specimens of *M. imporata* (Carpenter, 1864) from various depths and localities from Alaska to Baja California revealed them to be identical in all respects, except for a slight variation in the sculpture of the ribs of the head valve and lateral areas of intermediate valves. I thus recommend that *M. cithara* be treated as a synonym of *M. imporata*.

The new record extends the known range about 140 km to the south.

Mopalia lionota Pilsbry, 1918

Previous known distribution: San Pedro, Los Angeles County, California, to La Jolla, San Diego County, California (BURGHARDT & BURGHARDT, 1969), intertidal.

New records: Two specimens (one LACM 141168), 14.0 and 16.0 mm long, Punta Descanso, Baja California Norte, Mexico (32°14'N, 116°58'W), extreme low intertidal, in algal moss on top of large rocks. Collected by George A. Hanselman, 15 January 1980.

Two specimens (RNC), both 13.5 mm long, Government Point, 1 km S of Point Conception, Santa Barbara County, California (34°26.5'N, 120°27'W), intertidal in moss on tops of rocks. Collected by RNC, 22 November 1988.

One specimen (RNC), 24.0 mm long, Shell Beach, San Luis Obispo County, California (35°10'N, 120°40'W), intertidal on top of rock. Collected by RNC, 7 January 1986.

Three specimens (one LACM 141159), 16.5–20.5 mm long, Lighthouse Beach, Santa Cruz, Santa Cruz County, California (36°58'N, 122°03'W), intertidal on tops of rocks. Collected by RNC, 12 March 1989.

Remarks: The new records extend the known range 355 km to the north and about 80 km to the south.

Mopalia phorminx Berry, 1919

Previous known distribution: Gulf of Alaska to Santa Monica Bay, Los Angeles County, California (CLARK, 1983), 18–183 m.

New record: Two specimens (one LACM 141164), 9.0 and 11.0 mm long, Naked Island, Prince William Sound, Alaska (60°37.8'N, 146°23'W), 28–31 m on broken shell and gravel bottom. Collected by RNC, 10 April 1985.

Remarks: The new record extends the known range 125 km to the north.

Mopalia spectabilis Cowan & Cowan, 1977

Previous known distribution: Kodiak Island and Kenai Peninsula, Alaska (CLARK, 1983) to San Luis Obispo County, California (CLARK, 1983), intertidal to 10 m on bottoms of rocks.

New record: Three specimens (one LACM 141166), 27–40 mm long, Government Point, 1 km S of Point Conception, Santa Barbara County, California (34°26.5'N, 120°27'W), intertidal under rock ledges. Collected by RNC, 22 November 1988.

Remarks: *Mopalia spectabilis* is found on the bottoms of rocks and on rocky outcroppings and under ledges covered with the bright red, social ascidian *Metandrocarpa taylora* and red and yellow, encrusting, siliceous sponges (*Haliclona* spp.), upon which it apparently feeds.

The new record extends the known range 80 km to the south.

Mopalia sinuata (Carpenter, 1864)

Previous known distribution: Kachemak Bay, Kenai Peninsula, Cook Inlet, Alaska (BAXTER, 1983) to Monterey, Monterey County, California (BURGHARDT & BURGHARDT, 1969), intertidal to 200 m.

New record: One specimen (LACM 141160), 11.0 mm long, off Avila Beach, San Luis Obispo County, California (35°11.50'N, 120°45'W), 25 m on side of boulder covered with pink, encrusting, coralline algae (*Lithothamnium* sp.) Collected by RNC, 3 January 1986.

Remarks: *Mopalia sinuata* is usually found on the sides of rocks and boulders, in (often silty) crevices, covered with pink, encrusting coralline algae of the genus *Lithothamnium*. I have also collected specimens on the shells of living *Fusitriton oregonensis*, *Haliotis rufescens*, and *H. kamchatkana*.

The new record extends the known range 160 km to the south.

Mopalia swanii (Carpenter, 1864)

Previous known distribution: Shumagin Islands, Aleutian Islands, Alaska, to Malibu, Los Angeles County, California (BURGHARDT & BURGHARDT, 1969), intertidal.

New record: Five specimens (one LACM 141163), 28.0–41.0 mm long, Dutch Harbor, Unalaska Island, Aleutian Islands, Alaska (55°54'N, 166°31'W), intertidal on sides and tops of rocks. Collected by RNC, 30 August 1985.

Remarks: The new record extends the known range 385 km to the west.

Placiphorella borealis Pilsbry, 1892

Previous known distribution: Bering Island, Commander Islands, Bering Sea, USSR (PILSBRY, 1892) to Hokkaido Island, Japan (SAITO & OKUTANI, 1989), intertidal and shallow subtidal.

New record: Three specimens (one LACM 141155), 20–41 mm long, Korovin Bay, Atka Island, Aleutian Islands, Alaska (52°14'N, 174°18'W), intertidal and 12–18 m on bottoms of large rocks. Collected by RNC, 21 August 1985.

Remarks: SIRENKO (1973) reported that *Placiphorella borealis* broods its young in its pallial grooves; this is the only member of the Mopaliidae known to do this. An examination of the specimens from Atka did not reveal any young.

BERRY (1917b) described what he mistook to be this species in material dredged off Cape Rollin, Simushir Island, Kurile Islands, USSR, at 228 fathoms (416 m) by

the Albatross expedition in 1906. An examination of two of these specimens (SBMNH 35135) revealed them to be *Placiphorella pacifica* Berry, 1919. Thus, *P. borealis* is chiefly an intertidal species, but is also found subtidally to at least 18 m on rocks.

The new record extends the known range 1200 km to the east.

Placiphorella pacifica Berry, 1919

Previous known distribution: Sea of Okhotsk, USSR (YAKOVLEVA, 1952, as *Placiphorella ushakovi*, *vide* SMITH, 1975) to off Guaymas, Sonora, Mexico (Gulf of California) (SMITH, 1975), 155–2000 m.

New records: Two specimens (LACM uncatalogued), curled, eastern Indian Ocean, South Tasmanian Ridge (42°21'S to 47°18'S, 147°52'E to 147°51'E). Collected by *Eltanin*, Cruise No. 27, Station No. 1984, 24 February 1967. Trawled, 910–915 m.

One specimen, 22 mm long, examined through the kindness of the late Dr. Antonio J. Ferreira (on loan to him from R. Pena), from off Errazuia, Antofagasta Province, Chile (latitude and longitude unknown); depth and date not stated.

Remarks: In the Aleutian Islands, I have collected adults and juveniles (6.0–36.0 mm long) on large cobbles and boulders, and juveniles (6.0–10.5 mm long) on the giant abyssal barnacle *Balanus evermanni* at depths of 210–274 m.

TAKI (1954) described *Placiphorella albitestae* from 200–550 m off the Pacific coast of Honshu Island, Japan. A comparison of Taki's description and excellent figures with specimens of *P. pacifica* (including the lectotype, SBMNH 34394) demonstrated that they are identical in valve morphology and color, girdle setae structure, and radular characteristics. Thus, I recommend that *P. albitestae* be treated as a synonym of *P. pacifica*.

The new records indicate that *Placiphorella pacifica* is distributed throughout the Pacific Ocean, and in the eastern Indian Ocean.

Placiphorella rufa Berry, 1917

Previous known distribution: Kachemak Bay, Kenai Peninsula, Alaska (BAXTER, 1983) to Forrester Island, Alaska (BERRY, 1917a), intertidal to 45 m on rocks.

New records: Six specimens (RBCM 976-1064-5), 25–46 mm long, off Walters Point, Owen Bay, Sonora Island, British Columbia, Canada (50°18'N, 125°09'W), 29 m on rocks. Collected by P. Lambert, 1 August 1976.

One specimen (RBCM 976-1046-2), 24 mm long, Edward King Island, Barclay Sound, SW Vancouver Island, British Columbia, Canada (48°49.50'N, 125°12.50'W), 29 m. Collected by P. Lambert, 14 June 1976.

Remarks: In southeastern Alaska *Placiphorella rufa* is found on boulders, cobbles, and rock ledges covered with crustose, pink coralline algae (*Lithothamnium* spp.).

The new records extend the known range 680 km to the south.

Placiphorella velata Carpenter, in Dall, 1879

Previous known distribution: Forrester Island, Alaska (BERRY, 1917a) to Todos Santos Bay, Baja California Norte, Mexico (PILSBRY, 1892), intertidal to 18 m on bottoms of rocks and in crevices.

New records: Four specimens (RNC), 31–40 mm long, Saint Lazaria Island, Kruzof Island (56°55'N, 135°45'W), at the entrance to Sitka Sound, Baranof Island, Alaska, intertidal on bottoms of boulders. Collected by RNC, 2 June 1983.

Two specimens (one LACM 141156), 24 and 36 mm long, English Bay, Hichinbrook Island, Prince William Sound, Alaska (60°17.03'N, 146°40.07'W), intertidal in rock crevices. Collected by RNC, 15 April 1986.

Remarks: In Oregon this species is often found in sea urchin (*Strongylocentrotus purpuratus*) excavations in bedrock exposed to heavy surf.

Reports of *Placiphorella stimpsoni* (Gould, 1859) in Alaskan waters (BURGHARDT & BURGHARDT, 1969; PUTMAN, 1980; BAXTER, 1983, 1987) are misidentifications of *P. velata*.

The new records extend the known range 625 km to the north.

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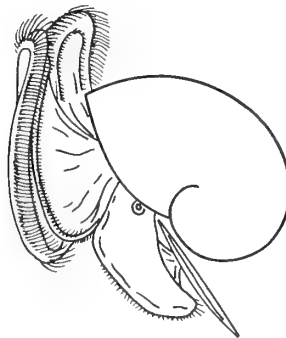
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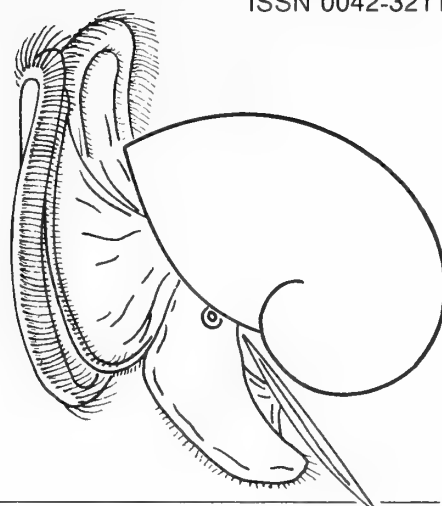
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Review of the Flabellinidae (Nudibranchia: Aeolidacea) from the Tropical Indo-Pacific, with the Descriptions of Five New Species

by

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Abstract. The morphology and systematics of seven members of the Flabellinidae are described and discussed. *Coryphella* Gray, 1850, and *Coryphellina* O'Donoghue, 1929, are maintained as synonyms of *Flabellina* Voigt, 1834. The morphological variability of *F. bicolor* (Kelaart, 1858) is fully described and *F. annuligera* (Bergh, 1900), *F. ornata* (Risbec, 1928), and *F. alisonae* Gosliner, 1980, are considered as synonyms. *Flabellina rubrolineata* (O'Donoghue, 1929) is recorded from several localities from Aldabra Atoll to Enewetak Atoll.

Five new species of *Flabellina* are described. *Flabellina riwo* sp. nov., *F. bilas* sp. nov., and *F. rubropurpurata* sp. nov. have perfoliate rhinophores and are closely allied to *F. bicolor*. Two other species, *F. delicata* sp. nov. and *F. exoptata* sp. nov., have papillate rhinophores and are most closely allied to *F. rubrolineata*, *F. poenicia*, and *F. marcusorum*.

The phylogeny of two clades of flabellinids is further elucidated, based upon the examination of several new taxa. The biogeography of the Flabellinidae is discussed relative to the proposed phylogenetic hypothesis.

INTRODUCTION

The Flabellinidae have received considerable attention in recent years (MILLER, 1971; KUZIRIAN, 1979; GOSLINER & GRIFFITHS, 1981; GOSLINER & KUZIRIAN, 1990), but the emphasis of most systematic treatments has been upon temperate species, rather than upon tropical members of the family.

Recent collections of opisthobranchs from several localities within the Indo-Pacific tropics, including Fiji, Australia, Papua New Guinea, the Seychelles, Madagascar and Aldabra, have brought to light specimens of seven species of Flabellinidae. The members of this family are poorly known in the Indo-Pacific and provide the focus of this systematic and morphological study.

SPECIES DESCRIPTIONS

Flabellina bicolor (Kelaart, 1858)

(Figures 1A, 2-5)

Eolis bicolor KELAART, 1858:115; KELAART 1859:490.

Aeolis bicolor (Kelaart, 1858): KELAART, 1883:104.

Samla annuligera BERGH, 1900:237, pl. 20, figs. 47-55.

Samla bicolor (Kelaart, 1858): ELIOT, 1906:685, pl. 45, fig. 4.

Coryphella ornata RISBEC, 1928:266, pl. 11, fig. 1, text fig. 89, nos. 1, 2; RISBEC, 1953:143, fig. 98a; BABA, 1936:44, fig. 26, pl. 2, fig. b., **syn. nov.**

Flabellina ornata (Risbec, 1928): BABA, 1955:29, fig. 48, pl. 15, figs. 42, 43; WILLAN & COLEMAN, 1984:42, fig. 134. **syn. nov.**

Flabellina alisonae GOSLINER, 1980:40, figs. 1, 2; BERTSCH & JOHNSON, 1981:88; JOHNSON & BOUCHER, 1984:283. **syn. nov.**

Flabellina ornata Angas: ORR, 1981:72. (*non Flabellina ornata* Angas, 1864). **syn. nov.**

Distribution: This species is widespread throughout the Indo-Pacific and is known from the Hawaiian Islands (BERGH, 1900; GOSLINER, 1980; BERTSCH & JOHNSON, 1981; present study), the Marshall Islands (JOHNSON & BOUCHER, 1984); Fiji (present study), New Caledonia (RISBEC, 1928); Guam (present study); Australia (WILLAN & COLEMAN, 1984); Okinawa (BABA, 1936; present study), Japan (BABA, 1955), Hong Kong (ORR, 1981), Papua New Guinea (present study), Sri Lanka (KELAART, 1858, 1859, 1883; ELIOT, 1906), the Seychelles (present study), Reunion (present study), Madagascar (present study) and South Africa (present study).

Material: Twelve specimens, California Academy of Sciences, San Francisco, CASIZ 070558, 1 dissected, N end Mahe Island, Republic of Seychelles, 21 April 1984, T. M. Gosliner. One specimen, CASIZ 070563, 1 km N of Mahe Beach Hotel, Mahe Island, Republic of Seychelles, 3 May 1984, T. M. Gosliner. Three specimens, CASIZ 070564, Anse Takamaka, Mahe Island, Republic of Seychelles, 2 May 1984, T. M. Gosliner. Ten specimens, CASIZ 070565, N of Beau Vallon, Mahe Island, Republic of Seychelles, 21 April 1984, T. M. Gosliner. One specimen, CASIZ 070559, lagoon between Passe Femme and Passe DuBois, Aldabra Atoll, Seychelles, 19 March 1986, T. M. Gosliner. Three specimens, CASIZ 070560, Middle Camp, Aldabra Atoll, Seychelles, 18 March 1986, T. M. Gosliner. Seven specimens, CASIZ 070561, 070562, 070610, Passe Femme, Aldabra Atoll, Seychelles, 19–23 March 1986, T. M. Gosliner. One specimen, CASIZ 070600, reef flat, NE of pass through reef 5 km WSW of Mora Mora Village, Madagascar, 8 April 1988, T. M. Gosliner. Six specimens, CASIZ 070601, near Sea Stack, NW side of Nosy Tanikely, Madagascar, 14 April 1989, T. M. Gosliner. Two specimens, CASIZ 070602, point on N side of Andilana Beach, Nosy Be, Madagascar, 15 April 1989, T. M. Gosliner. Two specimens, CASIZ 070603, point NW of Village Beach, Nosy Komba, Madagascar, 16 April 1989, T. M. Gosliner. One specimen, CASIZ 070566, Barracuda Point, Pig Island, Madang, Papua New Guinea, 13.7 m depth, 29 January 1988, T. M. Gosliner. Two specimens, CASIZ 070568, dissected, N side of patch reefs, N side of Kranket Island, Madang, Papua New Guinea, 22.7 m depth, 24 January 1988, T. M. Gosliner. One specimen, CASIZ 070569, dissected, Rempi Lagoon, N of Madang, Papua New Guinea, 13.7 m depth, 3 February 1988, T. M. Gosliner. One specimen,

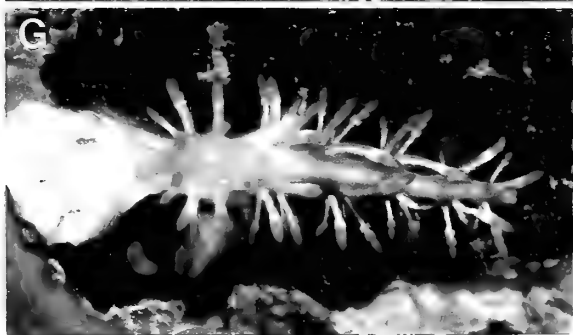
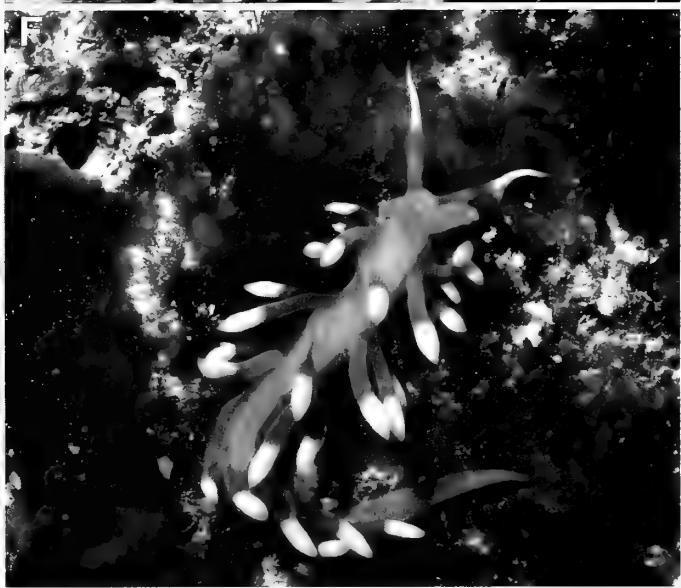
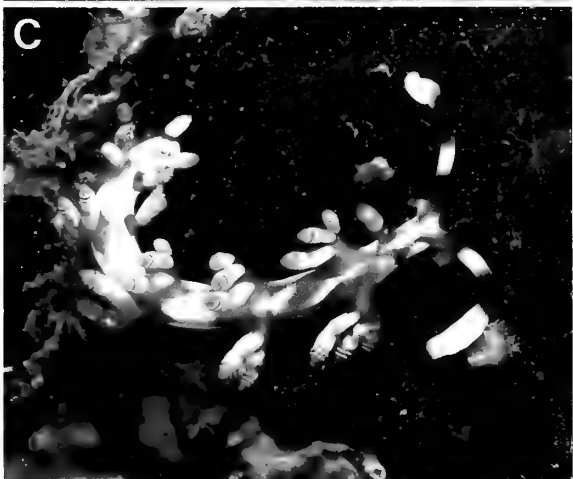
CASIZ 070604, Cement Mixer Reef, Madang, Papua New Guinea, 17 October 1986, T. Frohm. One specimen, CASIZ 070605, Cement Mixer Reef, Madang, Papua New Guinea, 6.1–7.6 m depth, 20 October 1986, M. Ghiselin. Three specimens, CASIZ 070606, Cement Mixer Reef, Madang, Papua New Guinea, 6 m depth, 19 October 1986, T. M. Gosliner. One specimen, CASIZ 070607, patch reef, N end Kranket Island, Madang, Papua New Guinea, 10.7 m depth, 1 October 1986, T. M. Gosliner. One specimen, CASIZ 070608, opposite lab, between Pig Island and Massis Island, Madang, Papua New Guinea, 15.2 m depth, 30 September 1986, T. M. Gosliner. One specimen, CASIZ 070609, near lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. Nine specimens, CASIZ 070567, intertidal, Kewalo Basin, Mamala Bay, Honolulu, Oahu, Hawaii, 7 February 1986, T. M. Gosliner. One specimen, South African Museum, NB 63, Natal, South Africa, 29 December, 1958. One specimen, Kings Headland, Caloundra, Sunshine Coast, N of Brisbane, Queensland, 6 m depth, 31 May 1981, P. Gofton. One specimen, channel between main islets, Shag Rock, NW of Point Lookout, North Stradbroke Island, Queensland, 10 m depth, 17 June 1981, R. C. Willan. One specimen, under coral slab, outer reef flat, W end of Heron Island, Capricornia Section, Great Barrier Reef, Queensland, low intertidal, 16 July 1981, R. C. Willan. One specimen, "The Nursery," NW side of Julian Rocks, off Cape Byron, New South Wales, 5 September 1987, C. Buchanan.

External morphology: The living animals (Figure 1A) reach a maximum length of 22 mm. The general body color is translucent white or bluish white. Opaque white pigment may be present sparsely or densely on the oral tentacles, head, notum, and cerata. This pigment may entirely overlie the translucent white notum or may be present as discrete patches, separated by areas of translucence, usually at the bases of the ceratal peduncles. Generally, the bases of the oral tentacles, rhinophoral stalks, and cerata are devoid of opaque white, even in the most heavily pigmented individuals. The rhinophoral stalks may be either opaque or translucent white. More distally, a brownish band is present in some individuals and the apical portion is cream or orange. A vivid orange spot or incomplete or complete ring is present subapically on each ceras. The upper and lower boundaries of the orange pigment are sharply demarcated.

The body is narrow and elongate. The notum is high and rounded in profile, continuing as a ridge to the tip of the tail. The tail is elongate and pointed. The oral tentacles are elongate, approximately three times the length of the rhinophores. The tentacles are usually laterally com-

Figure 1

Living animals. A. *Flabellina bicolor* (Kelaart, 1858). B. *F. riwo* sp. nov. C. *F. bilas* sp. nov. D. *F. rubropurpurata* sp. nov. E. *F. rubrolineata* (O'Donoghue, 1929). F. *F. exoptata* sp. nov. G. *F. delicata* sp. nov.



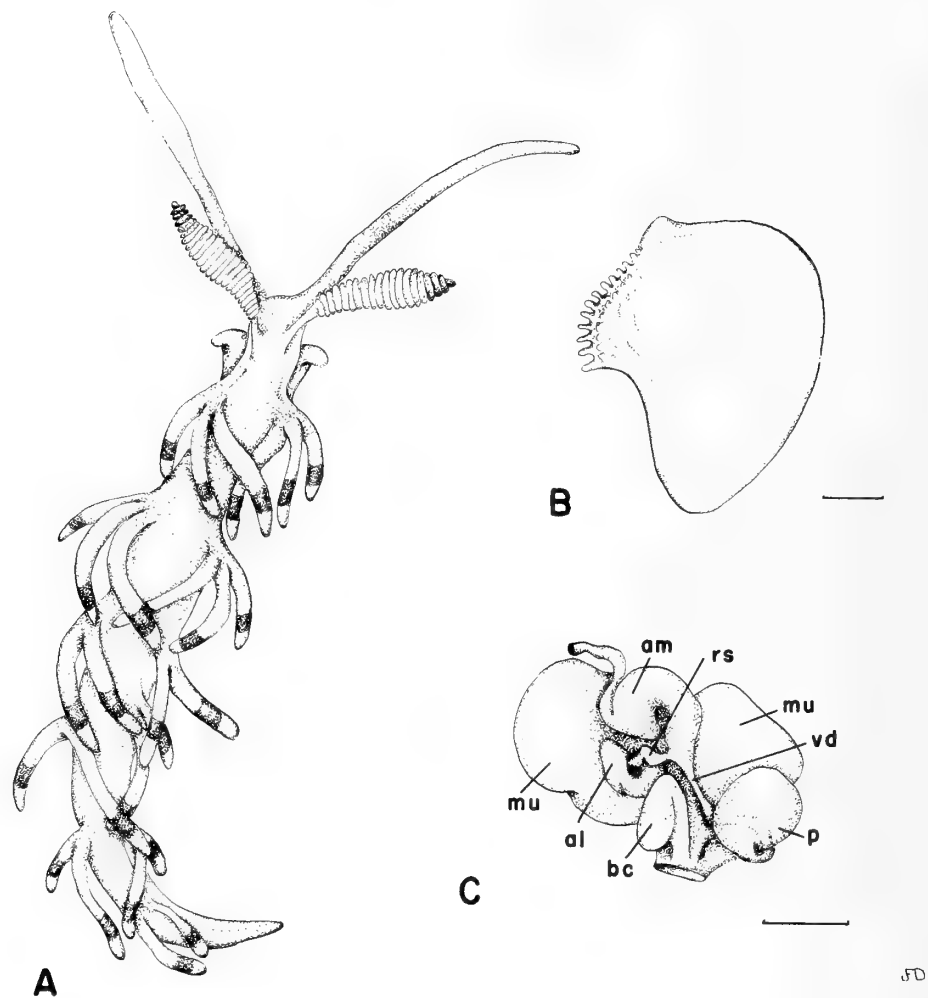


Figure 2

Flabellina bicolor (Kelaart, 1858). A. Dorsal view of 13 mm living animal. B. Jaw, scale = 0.1 mm. C. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; mu, mucous gland; p, penis; rs, receptaculum seminis; vd, vas deferens; scale = 0.3 mm.

pressed, but may become shorter and more cylindrical in animals held in aquaria for more than 24 hr. The rhinophores are perfoliate with 11–19 lamellae. The anterior foot corners are short, recurved and tentacular, but not acutely pointed. The cerata are generally held erectly in life. They are arranged in 4–8 discrete clusters per side of the body, each elevated on a short but distinct peduncle (Figure 2A). The precardiac and first 1–3 postcardiac rows each contain 3 or 4 cerata. The succeeding 2–4 posterior rows each contain 1 or 2 cerata. The gonopore is situated on the right side of the body, ventral to the anteriormost ceratal cluster. The pleuroproct anus is located immediately below the notal brim, between the precardiac and first postcardiac ceratal rows, nearer the postcardiac cluster (Figure 2A). The nephroproct is immediately dorsal to the anus.

Buccal mass: The buccal mass is short and muscular. From the anterior portion of the buccal mass, a pair of highly ramified oral glands extends posteriorly, and fills much of the first ceratal peduncle.

The jaws (Figure 2B) are thin and ovoid, with a well-developed masticatory border. The border (Figure 3A) bears approximately 3 rows of denticles. The outer row contains approximately 20 denticles, which are stronger and more prominent than the inner ones.

The radula (Figure 3B–D) has a formula of $14-20 \times 1 \cdot 1 \cdot 1 \cdot$ in the 10 specimens examined. The rachidian teeth (Figure 4) are evenly curved with a pair of elongate posterior limbs. There are 7–12 elongate denticles on either side of the longer, wider central cusp. When the rachidian tooth is viewed laterally (Figure 4D), the central cusp is higher than the adjacent denticles. The lateral teeth (Fig-

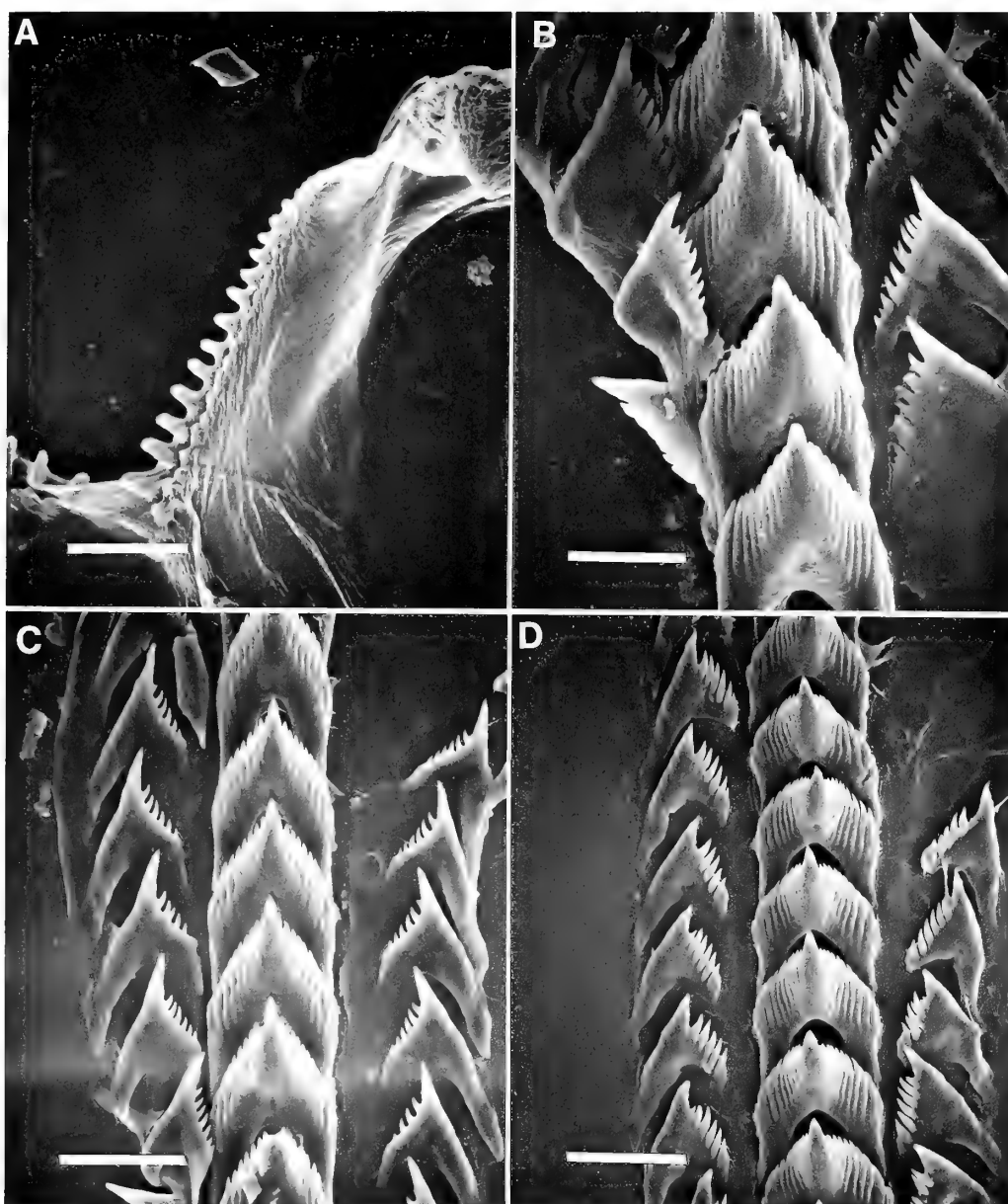


Figure 3

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs. A. Masticatory border of jaw, scale = 40 μm . B. Entire radular width, Oahu, Hawaii, scale = 20 μm . C. Entire radular width, Madang, Papua New Guinea, scale = 30 μm . D. Entire radular width, Mahe, Seychelles, scale = 40 μm .

ure 5) are broadly triangular with a basal portion of variable length. The primary cusp is triangular and acutely pointed. There are 4–10 denticles along the masticatory margin of the laterals. The size and number of denticles may vary considerably between specimens from a single locality.

Reproductive system (Figure 2C): The preampullary duct is elongate and narrow. It widens into a saccate am-

pulla. The ampulla divides into a short oviduct and a more elongate vas deferens. The oviduct widens into the serial receptaculum seminis (*sensu* EDMUNDS, 1970) and narrows again as it enters the albumen gland of the female gland mass. A small membrane gland is also present. The bulk of the female gland mass is composed of the mucous gland. Near the exit of the mucous gland into the genital aperture is a thick, recurved bursa copulatrix. The vas deferens widens into a curved prostatic portion. The pro-

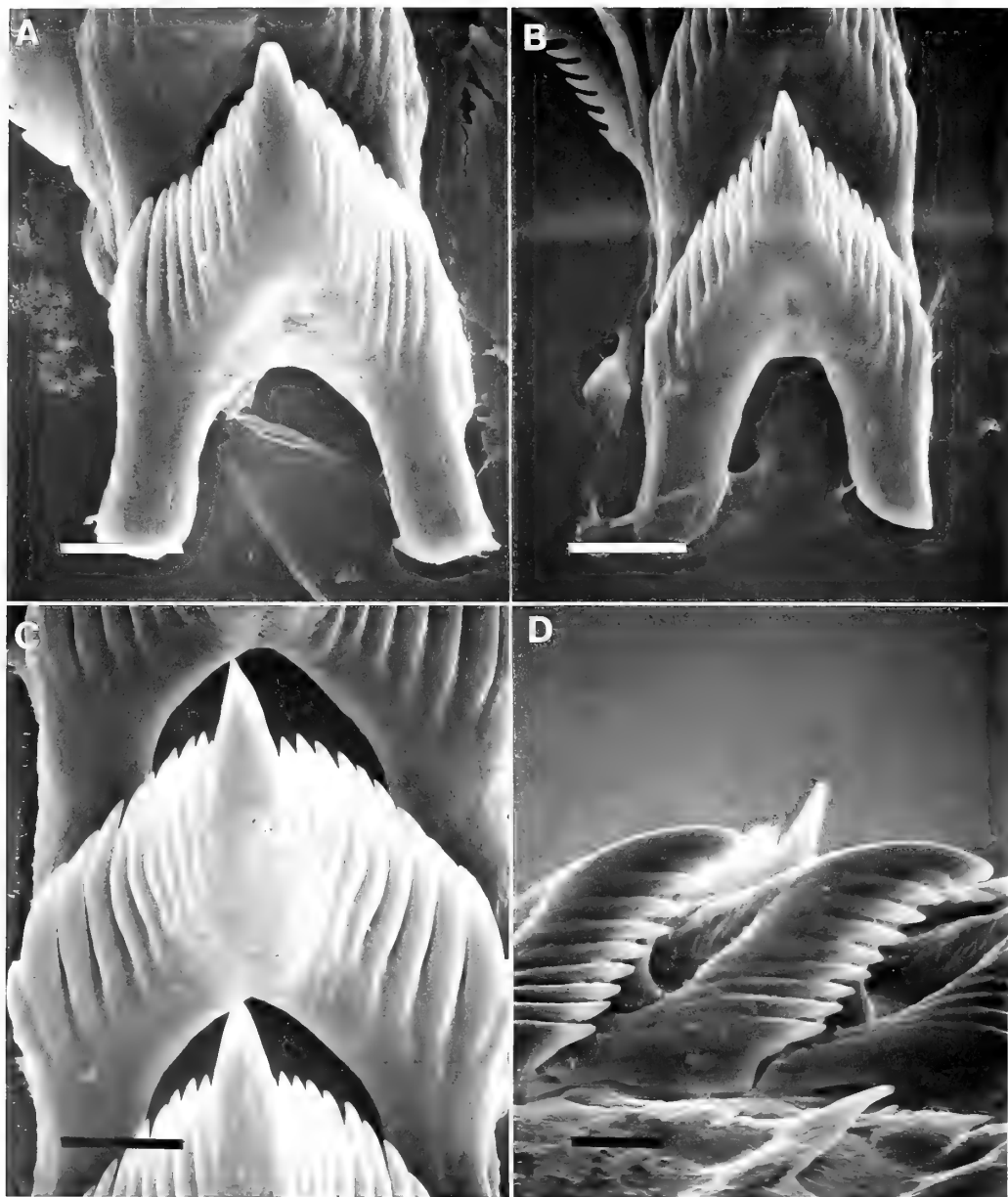


Figure 4

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs of rachidian teeth, scales = 10 μm . A. Dorsal view, Oahu, Hawaii. B. Dorsal view, Madang, Papua New Guinea. C. Dorsal view, Mahe, Seychelles. D. Lateral view, Madang, Papua New Guinea.

static portion exits directly into the short, indistinct penial papilla adjacent to the female gonopore.

Discussion: The systematic status of this widespread species has been poorly understood. Much of this confusion stems from the incomplete and often inaccurate original descriptions of *Eolis bicolor* Kelaart, 1858, *Samla annuligera* Bergh, 1900, and *Coryphella ornata* Risbec, 1928. BABA (1936, 1955) provided an accurate depiction of the mor-

phology of specimens from Okinawa and Japan. GOSLINER (1980) considered specimens from Hawaii as conspecific with Baba's animals, but distinct from both Bergh's and Risbec's species. On this basis *Flabellina alisonae* was described. The examination of specimens from much of the Indo-Pacific tropics provides an estimate of the range of variability of this species within and between populations. The color and ceratal arrangement of *E. bicolor*, *S. annuligera*, and *F. alisonae* are virtually identical. The only

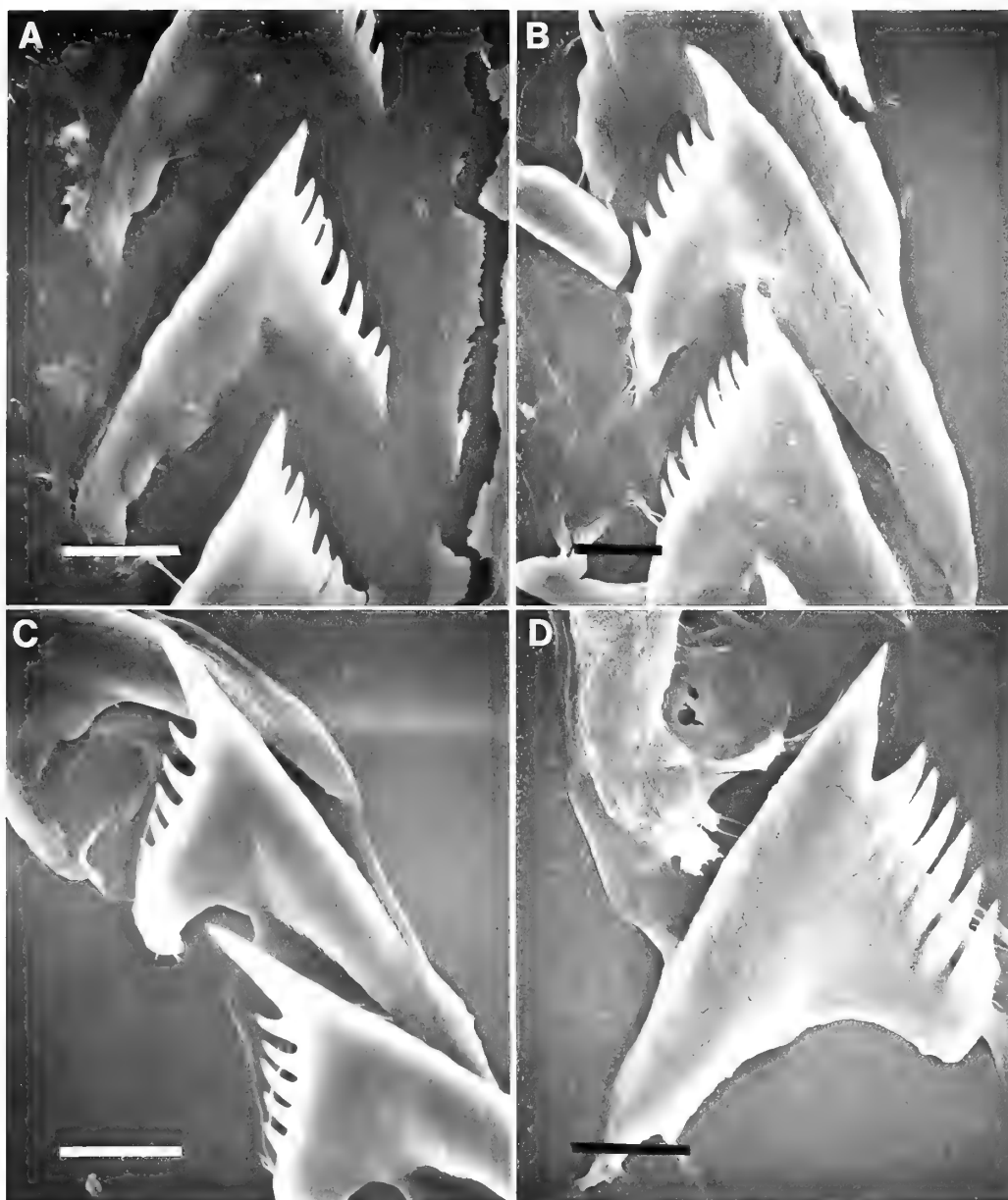


Figure 5

Flabellina bicolor (Kelaart, 1858), scanning electron micrographs of lateral teeth, scales = 10 μ m. A. Oahu, Hawaii. B, C. Madang, Papua New Guinea. D. Mahe, Seychelles.

significant differences between the three species are in the anterior end of the foot (stated to be rounded in *E. bicolor* and *S. annuligera* and tentacular in *F. alisonae*) and the number of rows of denticles on the masticatory border of the jaw (one in *F. annuligera* and two or three in *F. alisonae*). The corners of the foot may be difficult to differentiate when the animal has contracted during preservation. The difference in masticatory border of the jaw may be a result of a poorly prepared specimen where the secondary denticles were not visible. When separating the

jaws, part of the masticatory border often pulls away from the rest of the jaw. It may be that only the primary denticles of the border were present on the portion that Bergh illustrated. More importantly, no other member of the Flabellinidae has only a single row of denticles on the masticatory margin.

There are several apparent differences between *Eolis bicolor* and *Coryphella ornata* on one hand and *Flabellina alisonae* on the other. It is not apparent from either Kelaart's or Risbec's figure, or from the descriptions, that the

Table 1
Morphology of *Flabellina* species with perfoliate rhinophores.

Species	Color	Anterior right digestive branch	Radular rows	Denticles on inner laterals	Denticles on rachidian	Central cusp	Receptaculum seminis	Bursa copulatrix
<i>bicolor</i>	white to blue with orange rings on cerata	1 row	14–20	4–10	7–12	elevated	serial	recurved
<i>babai</i>	blue white with orange rings on cerata	2 rows	18–24	5–8	5–10	depressed	serial	absent
<i>bilas</i>	white with opaque white diamonds, red rings on cerata	1 row	21	2–4	9–10	depressed	serial	short stalk
<i>engeli</i>	orange with blue tinge and cream markings, cerata with orange bands	2 rows	19–20	5–10	7–11	depressed	semiserial	absent
<i>macassarana</i>	pink-yellow	2 rows	17	4–5	5	—	—	—
<i>riwo</i>	translucent white with opaque white network, blue rings on cerata	1 row	15–23	4–7	7–11	elevated	absent	reduced
<i>rubropurpurata</i>	body purple with red on cerata, rhinophores red	3	23–30	3–6	7–9	depressed	semiserial	stalked
<i>telja</i>	reddish with white spots	3–4 rows	14–28	6–9	6–11	depressed	semiserial	stalked

cerata are elevated from the notum on distinct peduncles. Also, the shapes of the jaws and radular teeth depicted by Risbec differ from those described by BABA (1936, 1955) and GOSLINER (1980). It should be noted, however, that Risbec's drawings are not known for their accuracy. The primary distinction between the two species cited by Gosliner, was the difference in ceratal arrangement. Gosliner interpreted the formula provided by Risbec as indicating that two precardiac rows of cerata are present on either side of the body. An alternative interpretation is possible. It appears that there may be two rows per side, with each row containing 3 cerata. The first of these rows could be precardiac, the second postcardiac. This would be consistent with the distribution of cerata observed in the present material.

Since the description of *Flabellina alisonae* from Hawaii (GOSLINER, 1980), several additional Indo-Pacific records of *Flabellina* specimens with orange ceratal rings have been published (BERTSCH & JOHNSON, 1981; JOHNSON & BOUCHER, 1984; ORR, 1981; WILLAN & COLEMAN, 1984). The only external differences in these specimens are the amount of opaque white pigment covering the surface of the animal and the completeness of the orange ceratal rings. The range of pigment variability of specimens may vary as much within a locality as between disparate localities. Generally, Hawaiian specimens lack any trace of opaque white pigment, while specimens from Australia and Papua New Guinea may be densely covered with this opaque pigment. Specimens collected from Nosy Be, Madagascar, varied from no opaque white pigment to being densely covered. The amount of orange pigment on the cerata

varies considerably within populations of specimens from Australia, Papua New Guinea, and Madagascar.

The remainder of the external and internal anatomy of specimens examined in this study varied only slightly and was not correlated to the coloration differences noted above. The radular and reproductive morphology are highly consistent within and between populations.

It would appear that the described differences between *Flabellina bicolor*, *F. annuligera*, *F. ornata*, and *F. alisonae* can be attributed to errors in the original descriptions of the former three species. It is more parsimonious to consider that a single species of *Flabellina*, which bears orange pigment on its cerata, is widespread in the Indo-Pacific tropics, in light of the widespread distribution and variability of the species described here. Therefore, *F. annuligera* (Bergh, 1900), *F. ornata* (Risbec, 1928), and *F. alisonae* Gosliner, 1980, are considered to be junior subjective synonyms of *F. bicolor* (Kelaart, 1858).

Two other species of *Flabellina* have orange ceratal rings, *F. engeli* Ev. Marcus & Er. Marcus, 1968, and *F. babai* Schmekel, 1970. Contrary to *F. bicolor*, both of these species have two precardiac rows of cerata per side (SCHMEKEL, 1970; EDMUNDS & JUST, 1983) and a depressed central cusp of the rachidian radular teeth. One of us (R.C.W.) has examined live specimens of *F. babai* from European waters. Jeff Hamann (personal communication) has provided us with photos of *F. engeli* from the Caribbean. The coloration of living specimens of these two species is strikingly different from that of *F. bicolor*.

The species of *Flabellina* with perfoliate rhinophores are compared in Table 1.

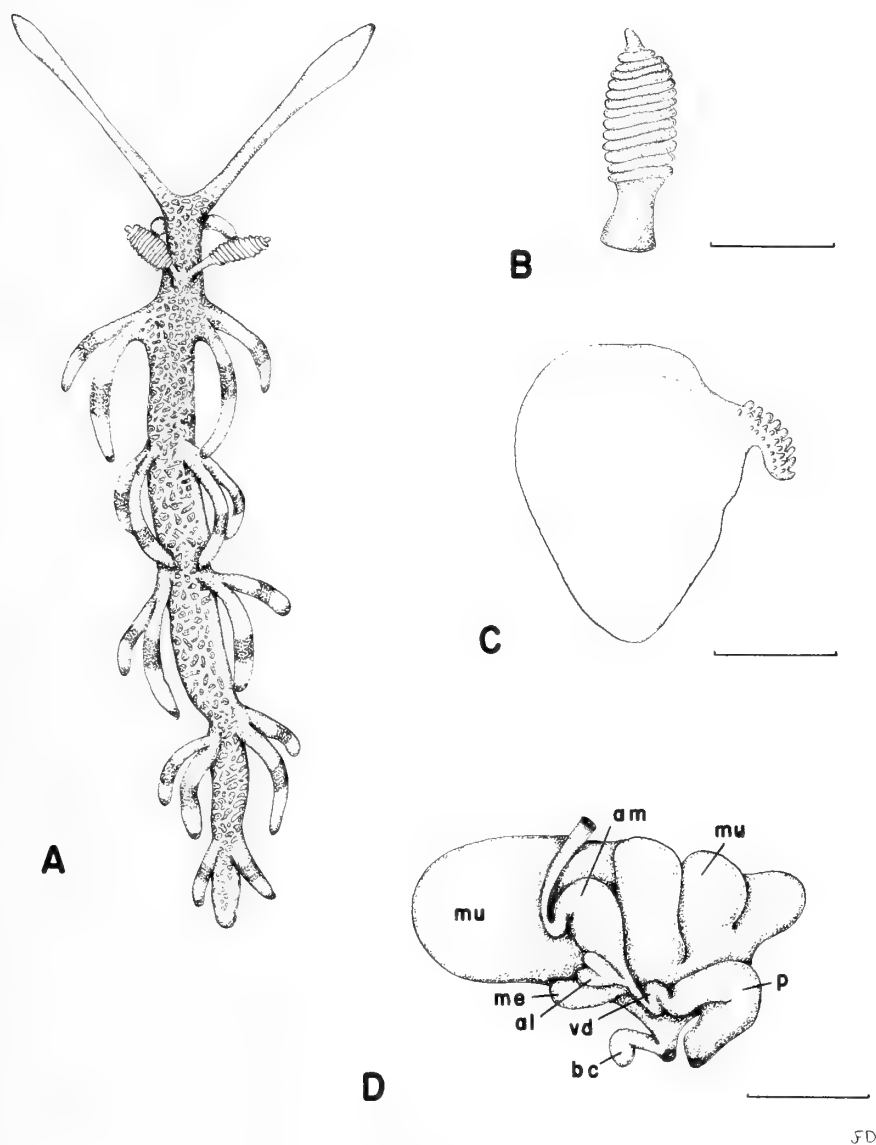


Figure 6

Flabellina riwo Gosliner & Willan, sp. nov. A. Dorsal view of 14 mm living animal. B. Rhinophore, scale = 1.0 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; vd, vas deferens; scale = 0.5 mm.

Flabellina riwo Gosliner & Willan,
sp. nov.

(Figures 1B, 6–8)

Distribution: This species is known from the northern coast of Papua New Guinea (present study), Manado, Sulawesi, Indonesia (Paulene Fiene-Severns, personal communication), Okinawa (Robert Bolland, personal communication), and the northeastern coast of Madagascar (present study).

Etymology: The epithet *riwo* refers to Riwo Village, approximately 15 km north of Madang, Papua New Guinea, where this species was first found.

Type material: Holotype, CASIZ 070952, Cement Mixer Reef, Madang, Papua New Guinea, 3 m depth, 18 October 1986, T. M. Gosliner.

One paratype, CASIZ 070953, between Pig Island and Massis Island, near Madang, Papua New Guinea, 15.2 m depth, 30 September 1986, T. Frohm. One paratype, CASIZ 070954, patch reef, Kranket Island, Madang, Papua New Guinea, 10.7 m depth, 1 October 1986, T. M. Gosliner. Three paratypes, CASIZ 070955, patch reef, Kranket Island, Madang, Papua New Guinea, 10.4 m depth, 4 October 1986, T. M. Gosliner. One paratype, CASIZ 070956, Rasch Pass, Madang, Papua New Guinea.

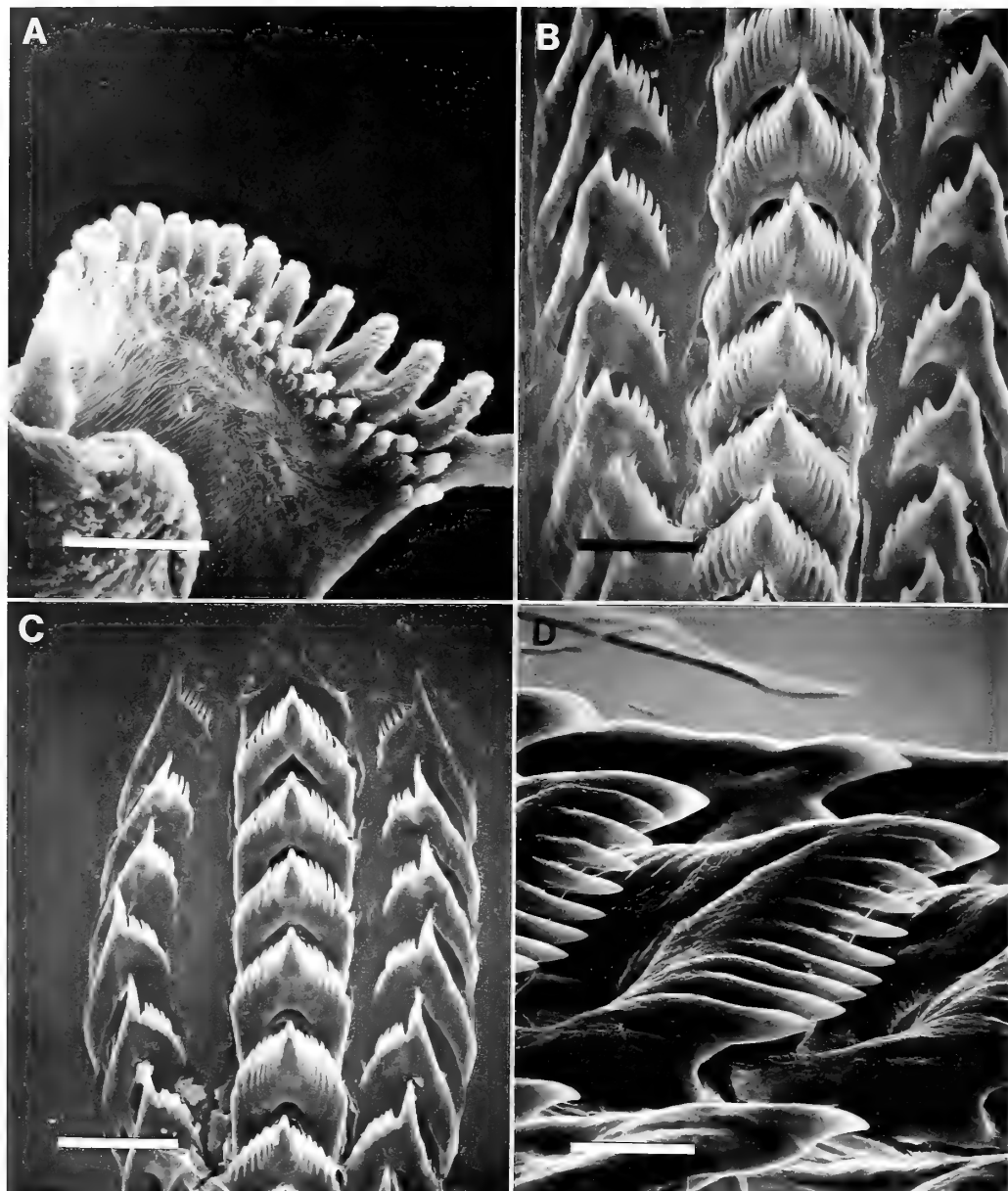


Figure 7

Flabellina riwo Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border of jaw, Nosy Be, Madagascar, scale = 20 μ m. B. Entire width of radula, Madang, Papua New Guinea, scale = 30 μ m. C. Entire width of radula, Nosy Be, Madagascar, scale = 40 μ m. D. Lateral view of rachidian teeth, Madang, Papua New Guinea, scale = 10 μ m.

ea, 12.2 m depth, 5 October 1986, T. M. Gosliner. One paratype, CASIZ 070957, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 6 October 1986, T. M. Gosliner. One paratype, CASIZ 070958, dissected, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 12.2 m depth, 8 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070959, lighthouse, Madang, Papua New Guinea, 12.2 m depth, 17 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070960, Cement

Mixer Reef, Madang, Papua New Guinea, 3 m depth, 18 October 1986, T. M. Gosliner. Two paratypes, CASIZ 070961, Cement Mixer Reef, Madang, Papua New Guinea, 6.1 m depth, 19 October 1986, T. M. Gosliner. Three paratypes, CASIZ 070962, Cement Mixer Reef, Madang, Papua New Guinea, 21 October 1986, T. M. Gosliner. One paratype, CASIZ 070968, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 15.2 m depth, 13 January 1988, T. M. Gosliner. Four paratypes, USNM

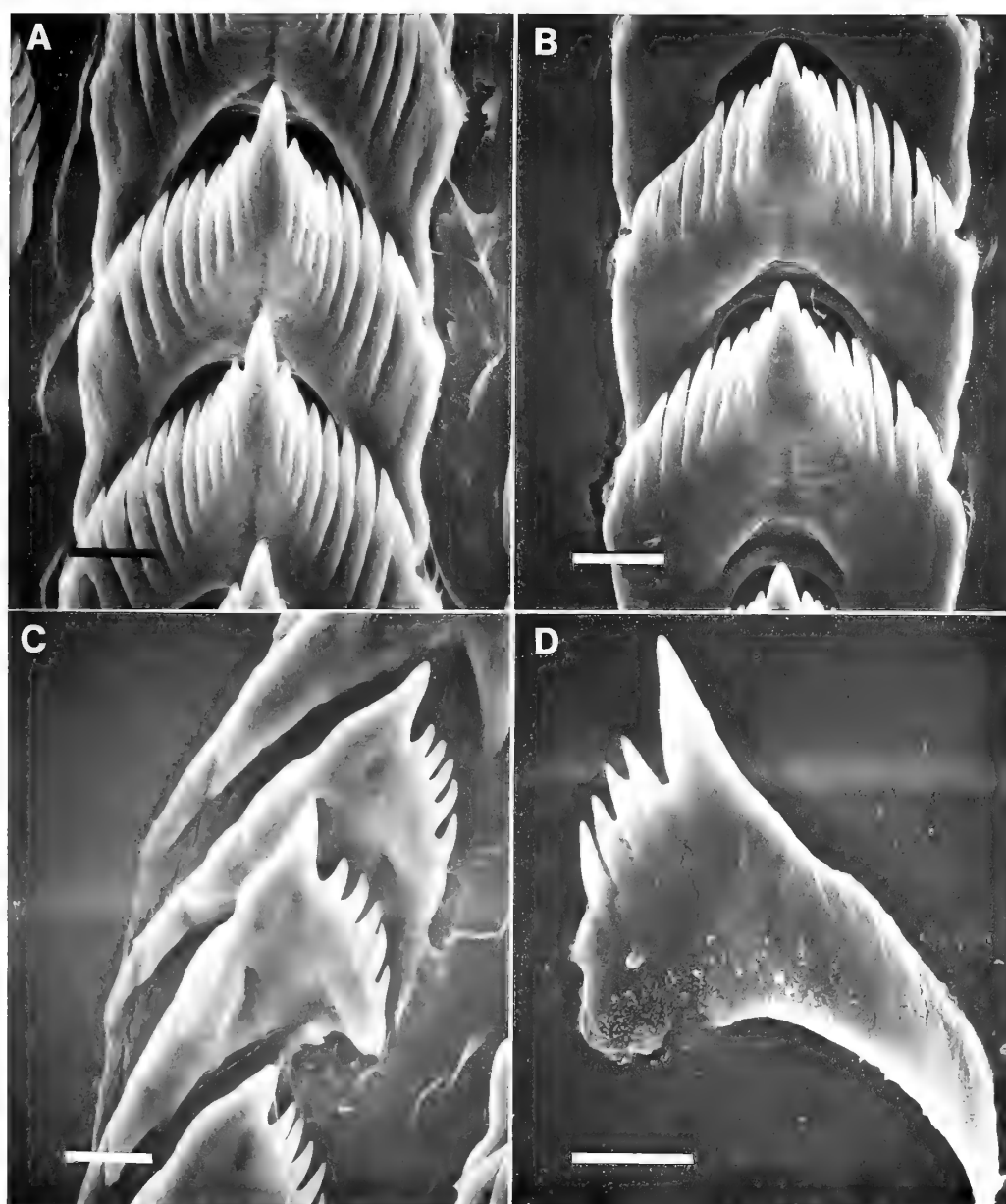


Figure 8

Flabellina riwo Gosliner & Willan, sp. nov., scanning electron micrographs, scales = 10 μ m. A. Dorsal view of rachidian teeth, Madang, Papua New Guinea. B. Dorsal view of rachidian teeth, Nosy Be, Madagascar. C. Lateral teeth, Madang, Papua New Guinea. D. Lateral tooth, Nosy Be, Madagascar.

859085, LACM 2465, ANSP A 13614, Australian Museum, AMS C164081, from same lot as previous specimen. Three paratypes, CASIZ 070969, lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. One paratype, CASIZ 070970, harbor wharf, Madang, Papua New Guinea, 10.4 m depth, 15 January 1988, T. M. Gosliner. Four paratypes, AMS C164082, coral rubble, the Quarry, near Bunu Village, 30 km N of Madang, Papua New Guinea, 3–5 m depth, 21 January

1988, R. C. Willan. Two paratypes, CASIZ 070971, dissected, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 24.4 m depth, 23 January 1988, T. M. Gosliner. Two paratypes, CASIZ 070972, patch reef off Kranket Island, near Madang, Papua New Guinea, 22.7 m depth, 24 January 1988, T. M. Gosliner. One paratype, CASIZ 070973, near the Pinnacle, between Pig Island and Rasch Pass, near Madang, Papua New Guinea, 30.5 m depth, 25 January 1988, T. M. Gosliner. One para-

type, CASIZ 070974, Hole in the Wall, near Hussein Village, N of Madang, Papua New Guinea, 15.2 m depth, 27 January 1988, R. C. Willan. One paratype, CASIZ 070975, Hole in the Wall, near Hussein Village, N of Madang, Papua New Guinea, 18.3 m depth, 3 February 1988, R. C. Willan. Two paratypes, CASIZ 070976, N point Christmas Bay, Bagabag Island, Papua New Guinea, 21.3 m depth, 5 February 1988, T. M. Gosliner and R. C. Willan. One paratype, CASIZ 070977, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 10.4 m depth, 8 February 1988, R. C. Willan. One paratype, CASIZ 070963, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 25 m depth, 16 July 1989, T. M. Gosliner. Two paratypes, CASIZ 070965, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 6.1 m depth, 31 August 1989, T. M. Gosliner. Three paratypes, CASIZ 070966, one dissected, Sea Stack, NW side Nosy Tanikely, Madagascar, 14 April 1989, T. M. Gosliner. Two paratypes, CASIZ 070967, one dissected, Cement Mixer Reef, Madang, Papua New Guinea, 3–7.6 m depth, 11 February 1989, T. M. Gosliner.

External morphology: The living animals (Figure 1B) reach a maximum of 20 mm in length. Most of the body is translucent white, adorned with a dense, lacy reticulum of opaque white lines. The oral tentacles are opaque white for most of their length, but possess a translucent basal portion near their junction with the head. The basal portion of the rhinophores is translucent white; the bulbous, lamellate portion is dull peach to light orange and the apex is translucent white. The base of the cerata may be either translucent white or obscured by opaque white pigment. When translucent, the cream, lobate digestive gland is visible. The apical portions of the cerata are covered with opaque white. Near the middle or in the distal third of each cerata is a broad purple ring.

The body is narrow and elongate (Figure 6A). The oral tentacles are three to four times the length of the rhinophores. The bases of the tentacles are terete whereas the distal third is markedly laterally compressed and paddle-shaped. The rhinophores (Figure 6B) are cylindrical basally and expand into a perfoliate club containing 16–22 densely crowded lamellae. The anterior foot corners are short, tentacular, and recurved. The cerata are arranged in 3–6 pedunculate clusters per side of the body. Each peduncle contains a single row of cerata inserted into an expanded portion of the notal brim. The notal brim is only evident in areas where the cerata are inserted. The peduncles contain 1–4 cerata. The ceratal formula varies considerably from small to large individuals. The first postcardiac row generally contains the largest number of cerata. The gonopore is located ventrally to the precardiac ceratal peduncle, on the right side of the body. The anus is situated between the precardiac and first postcardiac rows, generally closer to the more posterior peduncle. The

nephroproct is immediately dorsal or slightly anterior to the anal papilla.

Buccal mass: The anterior portion of the buccal mass forms a ring immediately inside the mouth. The paired ducts of the highly ramified oral glands originate from this area of the mass. These glands extend into the precardiac ceratal peduncle. The remainder of the buccal mass is highly muscular and contains the ovoid, chitinous jaws (Figure 6C). The masticatory border (Figure 7A) bears 3 or 4 distinct rows of denticles. The outermost row contains 18 elongate denticles with irregular papillae along their surface. The inner denticles decrease in size and papillation.

The radula (Figure 7B, C) has a formula of $15-23 \times 1 \cdot 1 \cdot 1$ in three specimens examined. The rachidian teeth (Figures 7D, 8A, B) are broad with an evenly curved posterior end. A deep cleft is present from the postero-medial end of the tooth to the base of the central denticle. The rachidian teeth bear 7–11 narrow denticles on either side of the more elongate central cusp. In lateral view, the central cusp of the rachidian is higher than the adjacent denticles (Figure 7D). The lateral teeth are roughly triangular with an elongate base. The primary denticle is elongate and acutely pointed. The masticatory border of the laterals bears 4–7 acutely pointed denticles.

Reproductive system (Figure 6D): The preampullary duct is narrow and expands into the saccate ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The oviduct does not expand into a discernible receptaculum seminis. It enters directly into the small albumen gland. The membrane gland is about the same size as the albumen gland and is situated immediately ventral to it. The mucous gland comprises the bulk of the female gland and forms the largest portion of the reproductive system. The mucous gland empties into the female gonopore adjacent to the small, thin-walled bursa copulatrix. The vas deferens expands abruptly into a short, thick prostatic portion that is contiguous with the penis. The penial papilla is simple and unarmed.

Discussion: *Flabellina riwo* differs markedly from *F. bicolor*. It is characterized by an opaque white network of pigment on the body as compared to a powdering of pigment in *F. bicolor*. The cerata bear a bluish purple ring rather than an orange one. Specimens of *F. riwo* generally have fewer cerata per cluster than does *F. bicolor*. Internally, *F. riwo* has broader rachidian teeth, with a distinct medial cleft, which is absent in *F. bicolor*. The reproductive system differs markedly between the two species; in *F. riwo*, there is no distinct receptaculum seminis and the bursa copulatrix is reduced, whereas in *F. bicolor*, both of these receptacles are well developed. The vas deferens is shorter in *F. riwo* than in *F. bicolor*. These differences are consistent throughout the extensive geographical ranges of the two species.

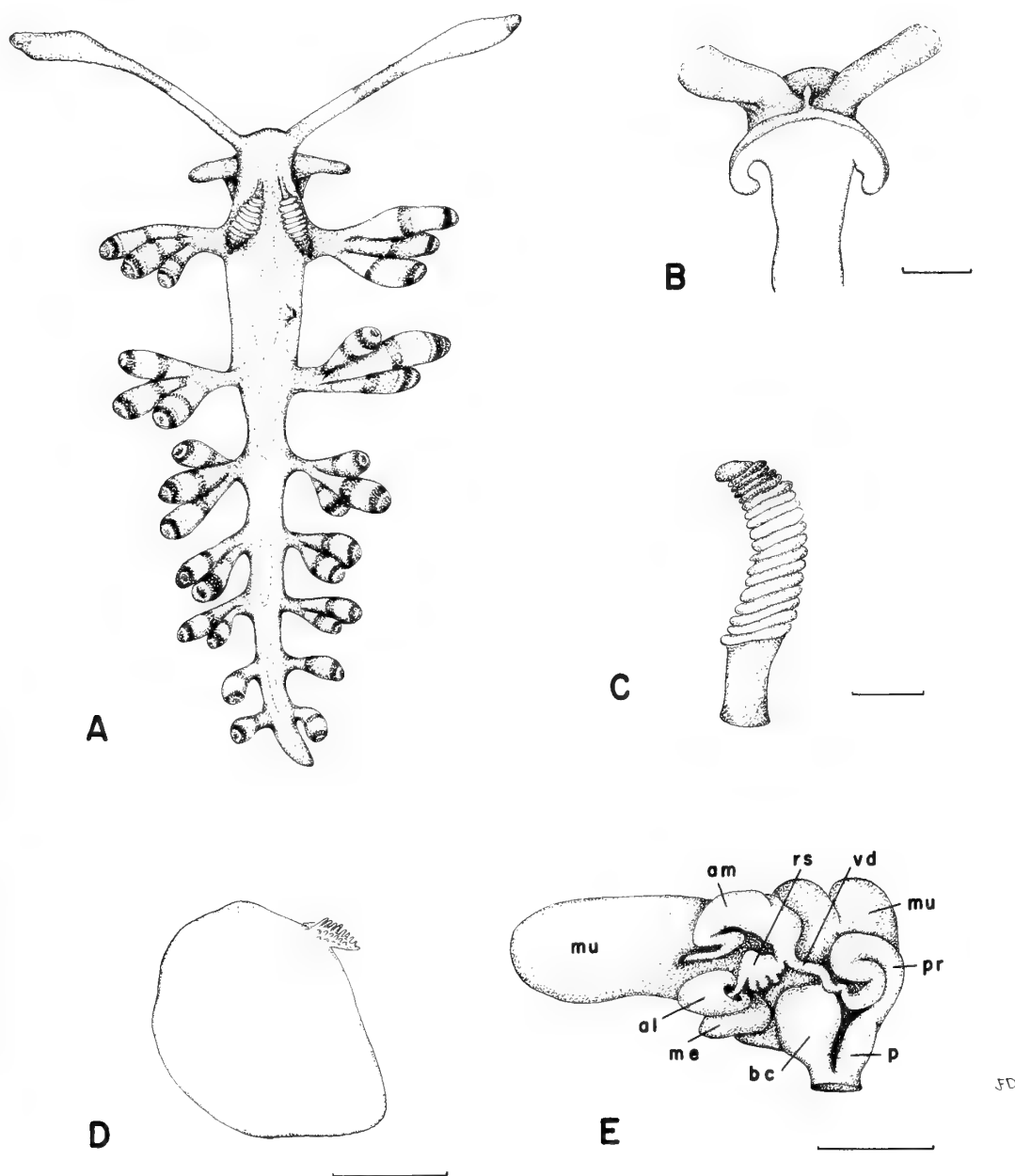


Figure 9

Flabellina bilas Gosliner & Willan, sp. nov. A. Dorsal view of 18 mm living animal. B. Ventral view of head and foot, scale = 1.0 mm. C. Rhinophore, scale = 0.5 mm. D. Jaw, scale = 0.2 mm. E. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; vd, vas deferens; scale = 0.5 mm.

Flabellina bilas Gosliner & Willan,
sp. nov.

(Figures 1C, 9–11)

Distribution: *Flabellina bilas* has been found from Kwajalein Island, Marshall Islands (Scott Johnson, personal

communication) and from Madang, Papua New Guinea (present study).

Material: Holotype, California Academy of Sciences, San Francisco, CASIZ 070993, living animal 17 mm in length, 20 m depth, Barracuda Point, Pig Island, near Madang,

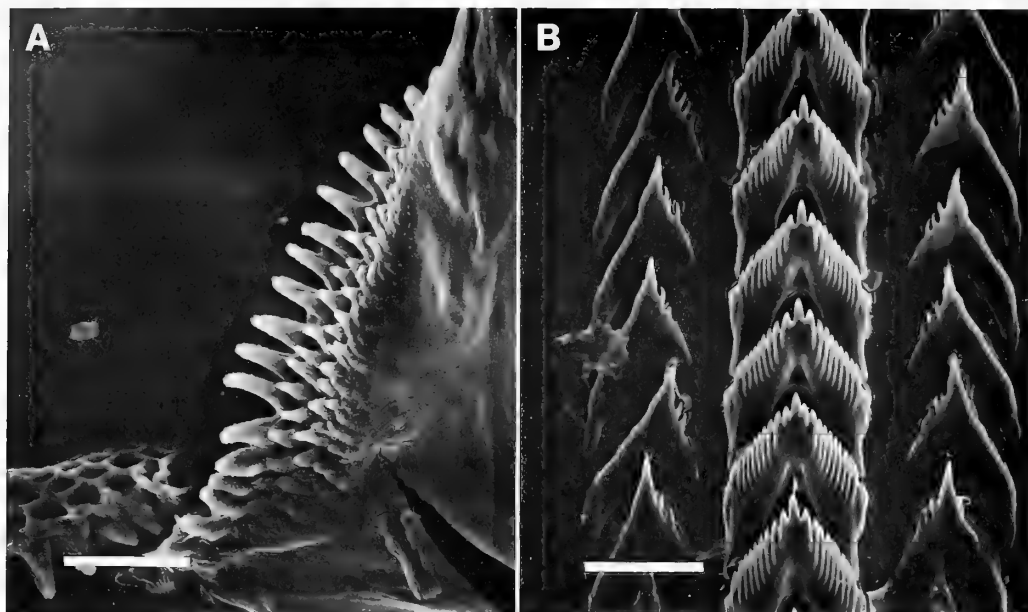


Figure 10

Flabellina bilas Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border, scale = 30 μm . B. Entire width of radula, scale = 50 μm .

Papua New Guinea, 8 February 1988, G. Williamson. Paratype, CASIZ 070994, living animal 23 mm in length, dissected, collected with the holotype.

Etymology: The specific epithet *bilas* is a New Guinea Pidgin word meaning "decoration," referring to the brilliant crimson and blue markings of this species.

External morphology: The living animals were 17 and 23 mm in length. The larger individual (the paratype) had lost the posterior portion of its body, perhaps as much as 3–4 mm. The living animals (Figure 1C) are vividly colored in a distinctive manner. The general body color is translucent white. There is an orange tinge on either lateral side of the head. The oral tentacles bear two opaque white areas, separating the translucent base, medial region, and apex. Opaque white pigment is also present on the foot corners and as a series of ovoid patches along either side of the body extending from the head to the tail. A series of sky-blue diamond or lozenge-shaped patches is present medially on the notum. These patches may be continuous or well separated. The rhinophores are translucent basally, medially, and apically. They possess two bands of opaque cream pigment and a sharply defined subapical blood-red ring. At the translucent base of some cerata a thin, blood-red digestive diverticulum is visible. More distally, are two broad areas of opaque cream separated by a small area of translucence. Subapically, a broad crimson ring is bordered on either side by a thinner irregular band of opaque white.

The animals are elongated and slender (Figure 9A). The oral tentacles are thin and elongate, approximately

three times the length of the rhinophores. The distal third of these tentacles is broadly expanded and paddlelike. The foot corners are short and tentacular, and are held nearly perpendicularly to the longitudinal axis of the body, or they may be recurved posteriorly. The anterior margin of the foot is bilabiate (Figure 9B). The perfoliate rhinophores (Figure 9C) bear 25–28 densely packed lamellae. The notal brim gives rise to a series of pedunculate cerata. There are 7 pairs of ceratal rows in the smaller, intact specimen. The larger one has 6 pairs of ceratal rows, but is missing the posterior portion of its body and tail. The ceratal formulae are: R 4,P,4,3,3,2,1, L 4,P,4,4,2,2,2 in the larger specimen and R & L 4,P,4,3,2,2,1,1 in the smaller individual. The gonopore is located immediately ventral to the preanal ceratal arch while the anus is situated slightly anterior to the median of the interhepatic space, below the notal brim. The nephroproct is immediately dorsal to the anus, but still below the notal brim.

Buccal mass: The buccal mass is highly muscular. From its anterior end emanates a pair of oral glands. These begin as simple ducts and branch many times into highly ramified glands, which are present in the precardiac ceratal peduncles. The jaws (Figure 9D) are thin and ovoid. Their masticatory border (Figure 10A) contains 4 or 5 rows of denticles. The outermost row bears approximately 20 elongate denticles. The denticles of the inner rows are increasingly short.

The radula (Figure 10B) has a formula of $21 \times 1 \cdot 1 \cdot 1$ in the paratype. The rachidian teeth (Figure 11A, B) are broad with 9 or 10 elongate denticles on either side of



Figure 11

Flabellina bilas Gosliner & Willan, sp. nov., scanning electron micrographs. A. Dorsal view of rachidian teeth, scale = 20 μ m. B. Lateral view of rachidian teeth, scale = 30 μ m. C. Lateral teeth, scale = 20 μ m.

the equally narrow central cusp. They are deeply indented posteriorly without a distinct medial cleft. When viewed laterally, the central cusp (Figure 11B) is depressed below the level of the adjacent laterals. The lateral teeth are triangular with an elongate base. The primary cusp is irregularly triangular and acutely pointed. The inner cutting edge bears 2–4 curved denticles.

Reproductive system (Figure 9E): The preampullary duct expands into the saccate ampulla. The ampulla nar-

rows and divides into the oviduct and vas deferens. The oviduct expands into a lobate serial receptaculum seminis and again narrows immediately prior to its entrance into the albumen gland. The albumen and membrane glands are small and are adjacent to each other. The mucous gland forms the bulk of the reproductive system and has a large lateral lobe. The mucous gland exits at the female gonopore. Adjacent to the gonopore is a large, bulbous bursa copulatrix with a short, thick stalk. The vas deferens is narrow for approximately half of its length and expands

into a coiled prostatic portion. The prostatic section is contiguous with the simple unarmed penis.

Discussion: *Flabellina bilas* can be readily distinguished from the other species with perfoliate rhinophores by its unique pattern of coloration. It is the only species with red bands on the cerata and rhinophores. Together with *F. engeli* Ev. Marcus & Er. Marcus, 1968, *F. bilas* has whitish or bluish markings on the notum, between the cerata. However, *F. engeli* has two precardiac ceratal rows (EDMUNDS & JUST, 1983) rather than one. The reproductive morphology also differs considerably. In *F. bilas* the receptaculum seminis is serial and the bursa copulatrix is present on a short stalk, whereas in *F. engeli* the receptaculum seminis is semiserial and the bursa copulatrix is apparently absent (Ev. MARCUS & ER. MARCUS, 1968).

Flabellina bilas is unique among described species of Indo-Pacific flabellinids with perfoliate rhinophores and a single precardiac ceratal row, in having a depressed cusp on the rachidian teeth.

Flabellina rubropurpurata Gosliner & Willan,
sp. nov.

(Figures 1D, 12–14)

Flabellina sp. 3: GOSLINER, 1987:114, fig. 223.

Distribution: This species is known from Natal, South Africa, Eniwetok, Marshall Islands (GOSLINER, 1987), and from Papua New Guinea (present study).

Etymology: The epithet *rubropurpurata* refers to the red cerata and purple body of this species.

Type material: Holotype, California Academy of Sciences, CASIZ 070995, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner.

Two paratypes, CASIZ 070996, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 12.2 m depth, 8 October 1986, T. M. Gosliner. One paratype, CASIZ 070997, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 10.4 m (maximum) depth, 12 February 1988, T. M. Gosliner. One paratype, CASIZ 070998, Barracuda Point, Pig Island, near Madang, Papua New Guinea, 24.4 m depth, 20 February 1988, T. M. Gosliner. One paratype, South African Museum, Cape Town, SAM A35718, radula only, 9 mile Reef, Sodwana Bay National Park, Natal, South Africa, 10 May 1981, T. M. Gosliner.

External morphology: The living animals (Figure 1D) are 4–9 mm in length. The general body color is a deep purple. The distal one-third to one-half of the oral tentacles is opaque white, while the basal portion is purple. The base of each rhinophore is purple; the central portion is opaque white and the distal third is red orange. Opaque white pigment is present along either edge of the notum from the level of the precardiac ceratal cluster to the pos-

terior end of the animal. The opaque white pigment may extend onto the lateral and dorsal surfaces of the animal. The cerata are purple basally and orange-red in the middle third; the apical cnidosac is orange.

The body (Figure 12A) is elongate and narrow. The notum is high and rounded in profile. The tail is elongate and pointed posteriorly. The oral tentacles are elongate, approximately twice the length of the rhinophores. They are rounded in cross section throughout their length, exhibiting no obvious lateral compression. The rhinophores (Figure 12B) are perfoliate with 12 or 13 densely packed lamellae. The anterior foot corners are short, tentacular, and may be extended perpendicularly to the body axis or may be curved. The cerata are short, fusiform, and thickest near the middle of their length. The cerata are arranged on distinct peduncles. The precardiac peduncle contains 3 distinct rows, with 2 or 3 cerata per row. The precardiac ceratal rows are crowded and difficult to differentiate in living specimens. There are 5–7 postcardiac ceratal peduncles per side, each consisting of a single row of 1–4 cerata. A distinct notal brim is absent between the peduncles. The gonopore is situated on the right side of the body, ventral to the third ceratal row of the precardiac peduncle. The pleuroproct anus is located immediately below the notum, between the precardiac and postcardiac ceratal peduncles. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The muscular buccal mass is small and occupies the anteriormost portion of the body cavity. Extending from the anterior end of the buccal mass are the paired ducts of the oral glands. The glands are highly ramified and occupy much of the precardiac ceratal peduncles. The jaws (Figure 12C) are thin and ovoid. They bear 2 or 3 rows of denticles on the surface of the masticatory border.

The radula (Figure 13) has a formula of $23-30 \times 1 \cdot 1 \cdot 1$ in the two specimens examined. The rachidian teeth (Figure 14A, B) are broadest posteriorly. The posterior limbs are elongate appendages used in articulation of the teeth with each other. The cutting edge of each tooth bears 7–9 elongate denticles on either side of the longer central cusp. In lateral view (Figure 13C) the central cusp of each rachidian tooth is depressed below the level of the adjacent denticles. The lateral teeth (Figure 14C, D) are elongate and triangular with a narrow base and extended primary cusp. There are 3–6 acutely pointed denticles on the masticatory border of the teeth.

Reproductive system (Figure 12E): The preampullary duct is short and narrow. It widens into the saccate ampulla, narrows again, and divides into the oviduct and vas deferens. After a short distance, the narrow oviduct gives rise to the pyriform, semiserial receptaculum seminis. From this point, the oviduct again narrows and enters the female gland mass near the albumen gland. The three portions of the female gland mass were not well differentiated from

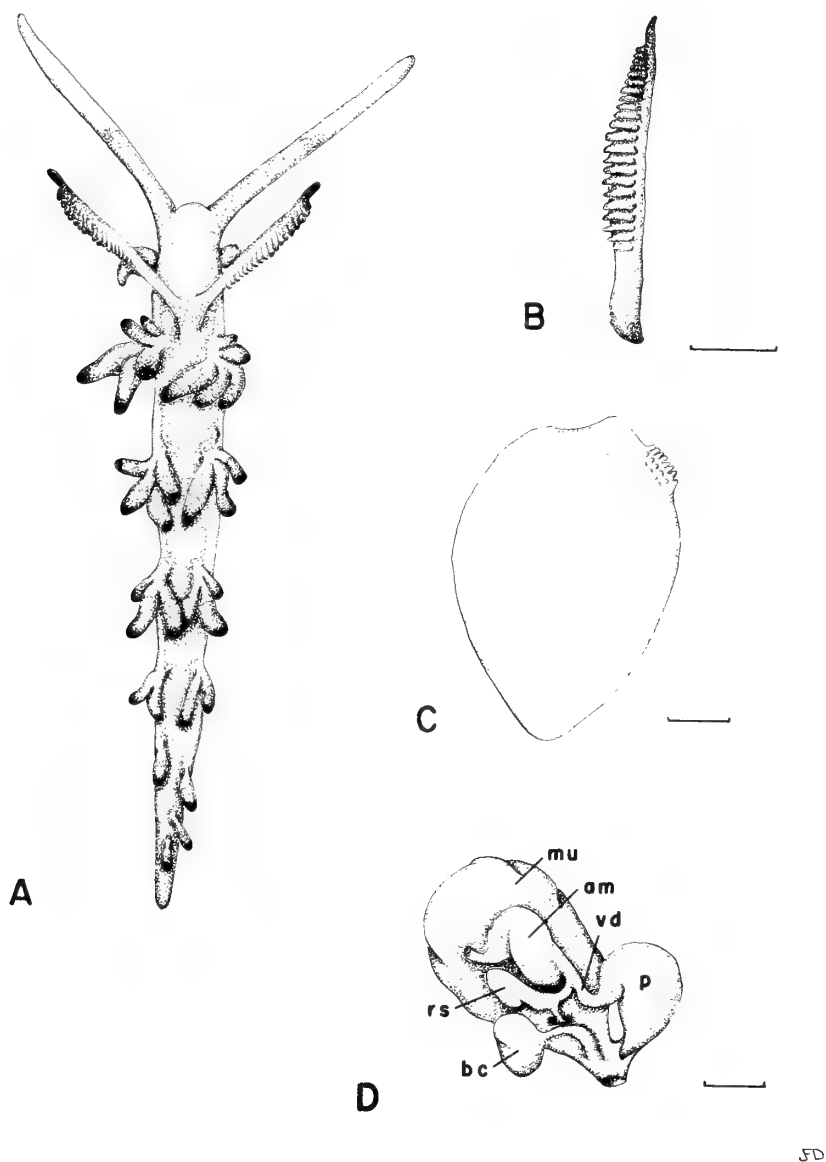


Figure 12

Flabellina rubropurpurata Gosliner & Willan, sp. nov. A. Dorsal view of 8 mm living animal. B. Rhinophore, scale = 0.5 mm. C. Jaw, scale = 0.1 mm. D. Reproductive system: am, ampulla; bc, bursa copulatrix; mu, mucous gland; p, penis; rs, receptaculum seminis; vd, vas deferens; scale = 0.1 mm.

each other. The female gland mass exits at the female genital aperture, adjacent to the bursa copulatrix. The bursa is spherical and exits via a long, narrow duct. The vas deferens is narrow and enlarges into the thick penis. No distinct prostatic portion of the vas deferens was observed. The simple unarmed penis terminates at the male gonopore.

Discussion: Based on a single specimen collected from southern Africa, GOSLINER (1987) indicated that the coloration of this species was distinct from all described spe-

cies of *Flabellina*. The arrangement of cerata, with three rows of cerata in the precardiac peduncle, is similar to that described for *F. telja* Er. Marcus & Ev. Marcus, 1967, and *F. stohleri* Bertsch & Ferreira, 1974.

Flabellina telja and *F. stohleri* are similar to each other in external morphology and coloration, and are sympatric within the Gulf of California. These two species are likely synonymous with each other. They differ in their coloration from *F. rubropurpurata*. These species are orange with opaque white spots and reddish cerata, whereas *F. rubropurpurata* has a purple body with reddish cerata.

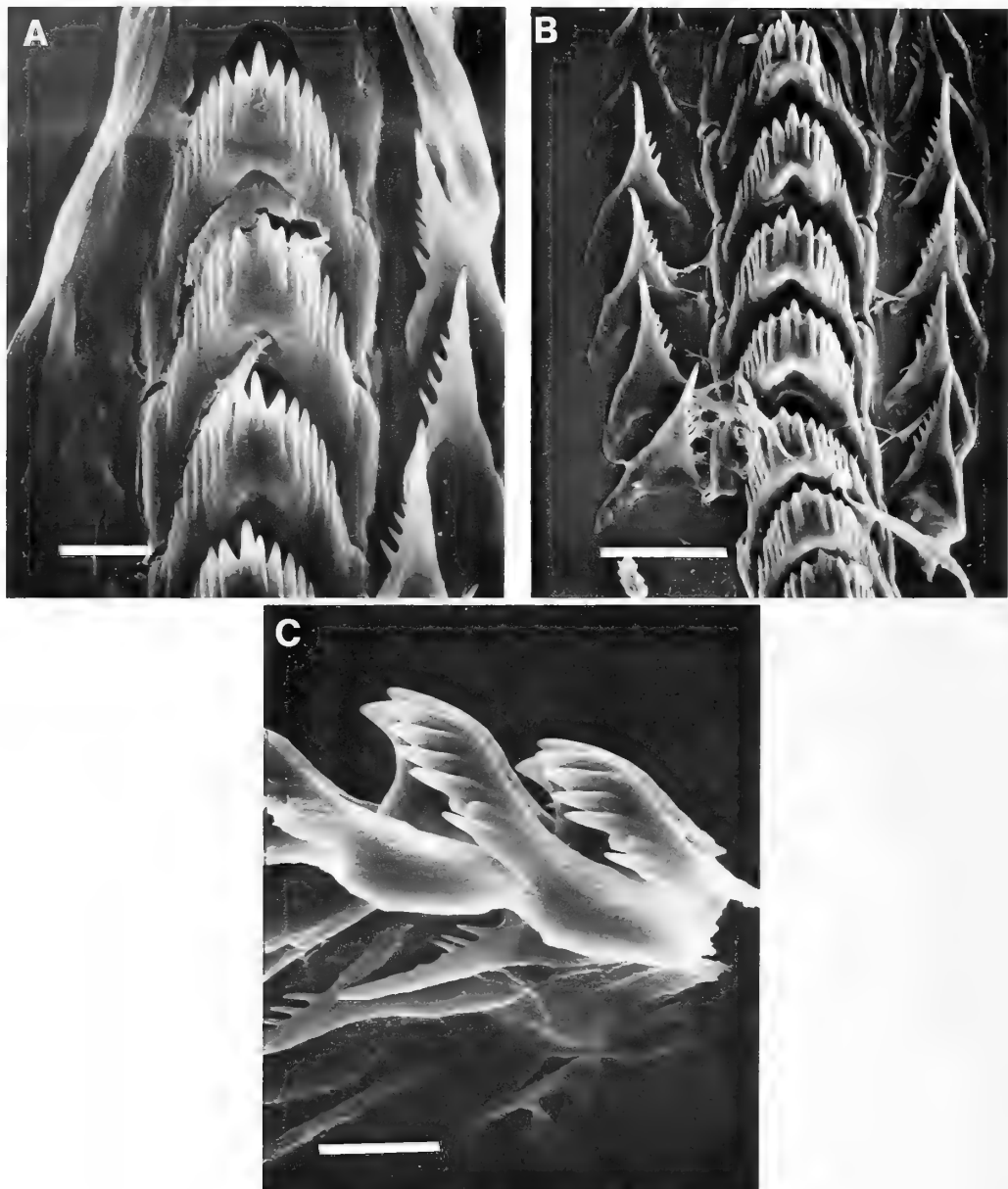


Figure 13

Flabellina rubropurpurata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Entire width of radula, Madang, Papua New Guinea, scale = 10 μ m. B. Entire width of radula, Sodwana Bay, South Africa, scale = 25 μ m. C. Lateral view of radula, Madang, Papua New Guinea, scale = 10 μ m.

Flabellina telja and *F. stohleri* have more cerata per row (up to 6) than *F. rubropurpurata* (maximum of 4). Internally, the lateral radular teeth of *F. telja* and *F. stohleri* possess more denticles than those of *F. rubropurpurata*. The male atrium of *F. telja* bears numerous papillae, whereas that of *F. rubropurpurata* is devoid of any ornamentation.

Flabellina rubrolineata (O'Donoghue, 1929)

(Figures 1E, 15–17)

Coryphella ornata RISBEC, 1928, in part: 267, variété violacée, fig. 89, 3; pl. 9, fig. 6. (This taxon has no systematic status because it was described as a vernacular name, see discussion).

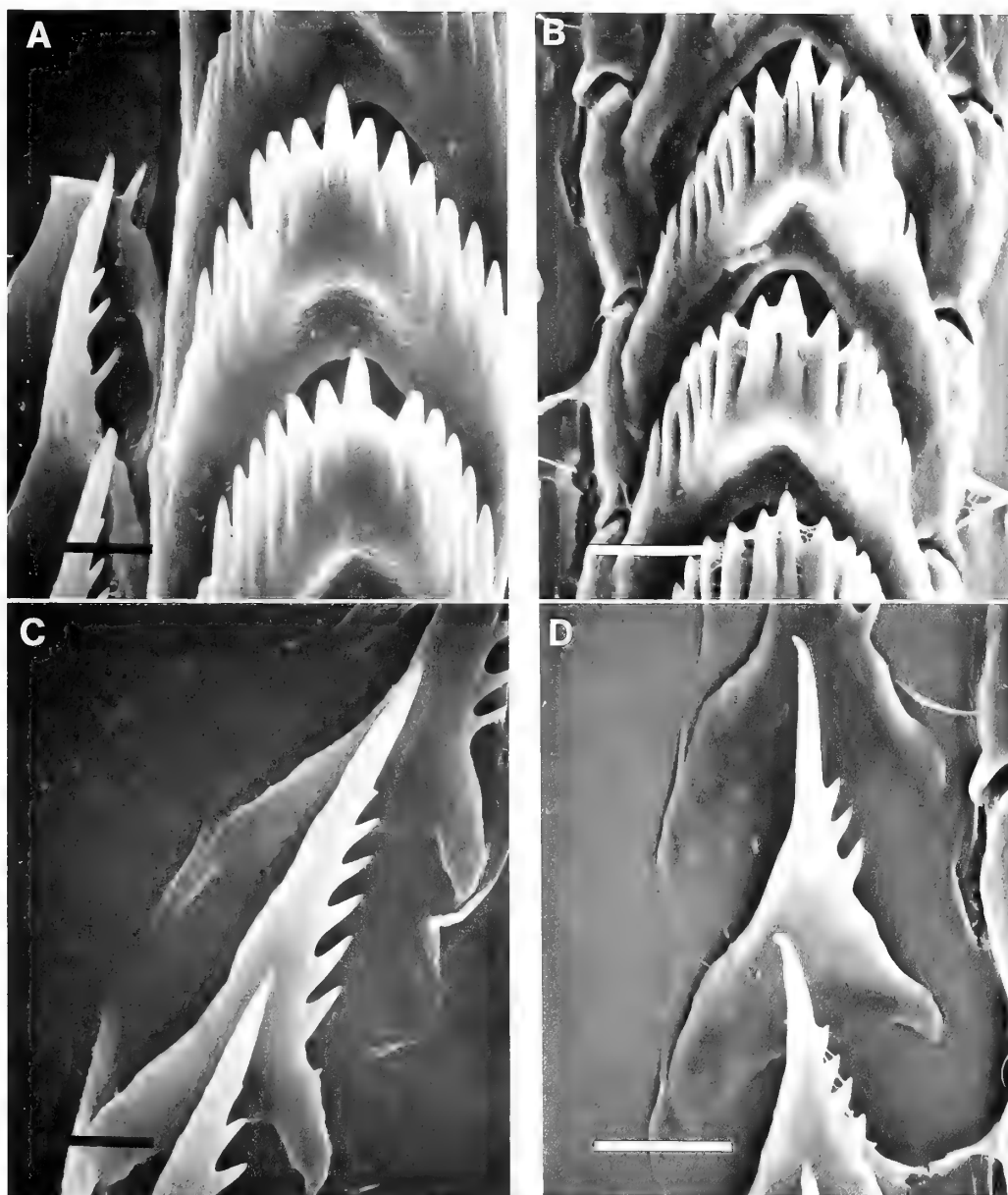


Figure 14

Flabellina rubropurpurata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Dorsal view of rachidian teeth, Madang, Papua New Guinea, scale = 5 μ m. B. Dorsal view of rachidian teeth, Sodwana Bay, South Africa, scale = 5 μ m. C. Lateral teeth, Madang, Papua New Guinea, scale = 5 μ m. D. Lateral teeth, Sodwana Bay, South Africa, scale = 10 μ m.

Coryphellina rubrolineata O'DONOGHUE, 1929:798, fig. 219; BABA, 1955:26, figs. 40, 41, pl. 13, fig. 37; BABA, 1990: 51, pl. 13, fig. 37.

Coryphella ornata var. *violacea* RISBEC, 1953:fig. 98a. **syn. nov.**

Coryphella violacea Risbec: GOSLINER, 1980:41. **syn. nov.**

Coryphella sp.: COLEMAN, 1981a:67, color fig.

Coryphella rubrolineata (O'Donoghue): COLEMAN, 1981b:31, color fig., 100.

Flabellina rubrolineata (O'Donoghue): GOSLINER & GRIF-FITHS, 1981:114; WILLAN & COLEMAN, 1984:42, fig. 133; MIENIS & GAT, 1986:683; GOSLINER & KUZIRIAN, 1990:9, fig. 6.

Distribution: This species is widely distributed in the Indo-Pacific tropics where it is known from New Caledonia (RISBEC, 1928), Australia (WILLAN & COLEMAN,

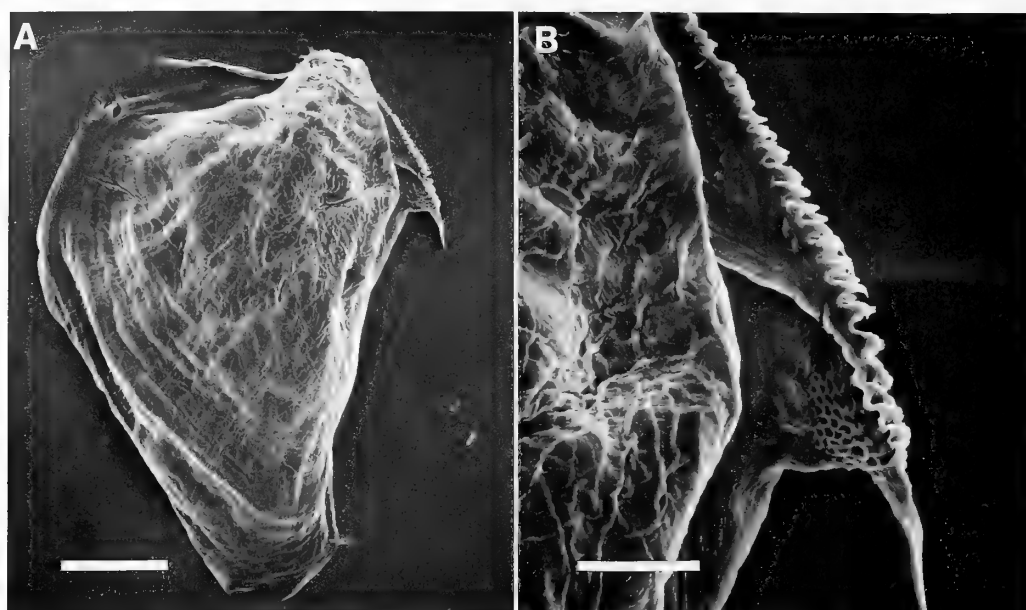


Figure 15

Flabellina rubrolineata (O'Donoghue, 1929), scanning electron micrographs. A. Jaw, Madang, Papua New Guinea, scale = 150 μm . B. Masticatory border, Madang, Papua New Guinea, scale = 40 μm .

1984), Japan (BABA, 1955), Papua New Guinea (GOSLINER & KUZIRIAN, 1990; present study), Malaysia (Ho Soon Lin, personal communication), Aldabra Atoll (present study), and the Red Sea (O'DONOGHUE, 1929; MIENIS & GAT, 1986; Christopher Todd, personal communication).

Material: One specimen, California Academy of Sciences, San Francisco, CASIZ 070557, Passe Femme, Aldabra Atoll, Republic of Seychelles, 19 March 1986, T. M. Gosliner. Four specimens, CASIZ 070547, 070549, 070550, Barracuda Point, Pig Island, Madang, Papua New Guinea, 10–27 m depth, 29 January–14 February 1988, T. M. Gosliner. One specimen, CASIZ 070553, Barracuda Point, Pig Island, Madang, Papua New Guinea, 6 October 1986, T. M. Gosliner. Two specimens, CASIZ 070556, SE side of Barracuda Point, Pig Island, Madang, Papua New Guinea, 24.4 m depth, 23 January 1988, J. Mizeu. One specimen, CASIZ 070548, Sek Passage, Madang, Papua New Guinea, 10.7 m depth, 15 October 1986, T. M. Gosliner. One specimen, CASIZ 070551, N side Rasch Pass, Madang, Papua New Guinea, 18.3 m depth, 16 February 1988, T. M. Gosliner. Three specimens, CASIZ 070552, the Quarry, 30 km N of Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner. Three specimens, CASIZ 070554, Kranket Wall, E side of Kranket Island, Madang, Papua New Guinea, 30.5 m depth, 4 February 1988, R. C. Willan. One specimen, CASIZ 070555, near lighthouse, Madang, Papua New Guinea, 12.2 m depth, 17 October 1986, T. M. Gosliner.

One specimen, "The Nursery," N side of Julian Rocks,

off Cape Byron, New South Wales, Australia, 6 m depth, 12 July 1980, R. C. Willan. Two specimens, in channel between main islands, Shag Rocks, off Point Lookout, North Stradbroke Island, Queensland, Australia, 13 m depth, 5 August 1980, R. C. Willan. Two specimens, base of Heron Bommie, W side Heron Island, Capricornia Group, Great Barrier Reef, Queensland, Australia, 10 m depth, 13 November 1980, R. C. Willan.

External morphology: The living animals (Figure 1E) reach 42 mm in length. The coloration is variable, even within a population from a single locality. The general body color is translucent pinkish white. Varying amounts of opaque white may be present on the sides of the body and notum. Three purple or reddish longitudinal lines extend from the head to the posterior limit of the tail. One of these is middorsal and extends from the anterior border of the head to the tail. A lateral line runs below the notum along either side of the body. Purple pigment may also be present on the distal third of the oral tentacles, on the apices of the foot corners, on the apices of the rhinophores, and on the cerata. The anterior face of the rhinophores is the same color as the body. Their posterior surface, where the papillae are situated, is opaque white or yellow. The cerata are translucent white or opaque white basally with red, purple, or yellow pigment on the distal portion. In one specimen from Papua New Guinea, the entire surface of the cerata was red.

The body is narrow and elongate. The notum is high and well developed and its brim undulate, widening at the level of each ceratal group. The oral tentacles are thin and

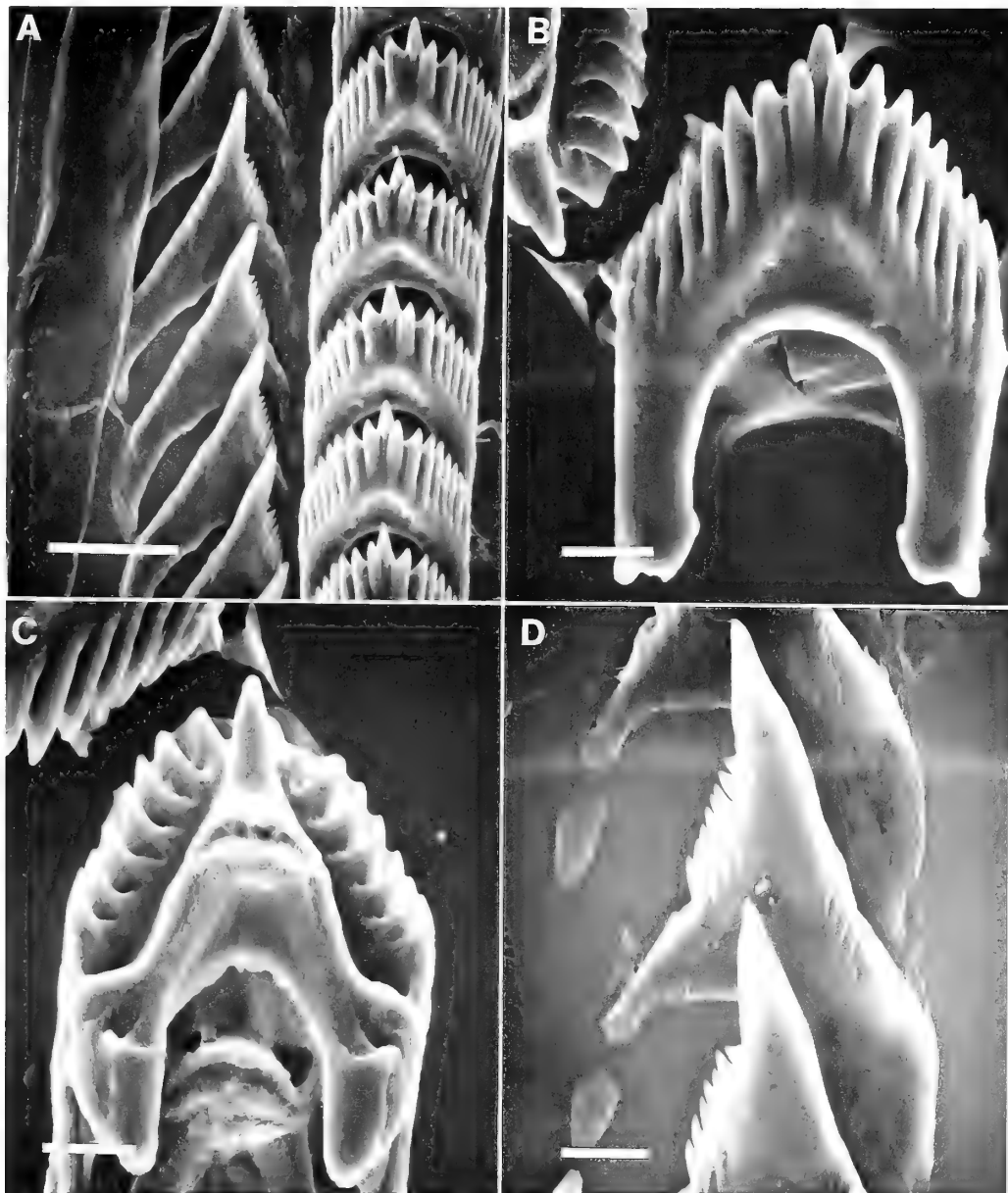


Figure 16

Flabellina rubrolineata (O'Donoghue, 1929), scanning electron micrographs. A. Rachidian and lateral teeth, Madang, Papua New Guinea, scale = 30 μm . B. Dorsal view of rachidian teeth, Madang, Papua New Guinea, scale = 10 μm . C. Ventral view of rachidian tooth, Madang, Papua New Guinea, scale = 10 μm . D. Lateral teeth, Madang, Papua New Guinea, scale = 10 μm .

cylindrical in cross section, longer than the rhinophores. The rhinophores are elongate with an acute apex. The posterior surface is ornamented with approximately 100 elongate papillae. The anterior foot corners are elongate and tentacular. The cerata are variable in length and may be short and bulbous or elongate and cylindrical. The cerata are arranged in 5 or 6 distinct groups, each elevated from the notum. The precardiac cluster consists of 3 or 4

distinct rows of cerata, with 1–3 cerata per row. The first 3 or 4 postcardiac groups are arranged in arches consisting of 3–6 cerata per arch. The posterior 1 or 2 clusters consist of only 1 or 2 cerata. The gonopore is situated ventral to the 2 posterior ceratal rows of the precardiac ceratal group. The pleuroproctical anus is located in the interhepatic space, below the notum. The nephroproct is immediately antero-dorsal to the anus, but still below the notal brim.

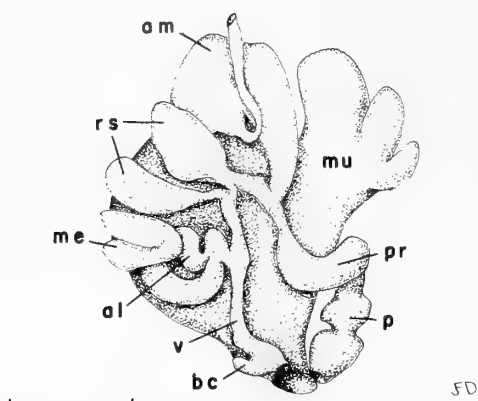


Figure 17

Flabellina rubrolineata (O'Donoghue, 1929). Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; scale = 0.5 mm.

Buccal mass: The muscular buccal mass is ovoid and occupies the portion of the body cavity anterior to the rhinophores. The large ramified oral glands emanate from the anterior portion of the buccal mass and extend posteriorly along the mass and into the notal expansions of the precardiac ceratal cluster. The jaws (Figure 15A) are well developed and thick. The masticatory border (Figure 15B) is broad and elongate, bearing 5–7 rows of denticles.

The radula (Figure 16A) has a formula of $29-30 \times 1 \cdot 1 \cdot 1$ in three specimens examined. The rachidian teeth (Figure 16B, C) are broad, with a wide arch between the posterior limbs. The posterior end of either limb has an articulatory appendage on its outer side. The cutting edge of the rachidian teeth has 7 or 8 denticles on either side of the more elongate central cusp. The central cusp is depressed below the level of the adjacent denticles. The lateral teeth (Figure 16D) are broadly triangular with an elongate, curved basal limb. There are 7 or 8 acutely pointed denticles along the inner margin of the laterals. The outer side of the teeth bears 4 or 5 irregular striations.

Reproductive system (Figure 17): The arrangement of the organs is triaulic. The preampullary duct is narrow and elongate. It expands into a wide, saccate ampulla, which again narrows and divides into the oviduct and vas deferens. After a short distance, the oviduct gives rise to two distinct pyriform receptacula seminis. From this point the oviduct continues towards the gonopore and enters the albumen gland portion of the female gland mass. The membrane gland is situated adjacent to the albumen gland. Most of the female gland mass is formed by the various lobes of the mucous gland. From the point where the oviduct enters the female gland mass, a vaginal duct extends to its own aperture, adjacent to the penis. A minute bursa copulatrix is present adjacent to the vaginal pore. The opening of the mucous gland is immediately ventral

to the vaginal pore. The vas deferens expands into a short prostatic portion, which widens again at the conical, unarmed penial papilla.

Discussion: When it was described, *Coryphellina* O'Donoghue was monotypic, its type species being *Coryphellina rubrolineata* O'Donoghue, 1929. *Coryphellina* has been considered as a junior synonym of *Coryphella* Gray, 1850, by MILLER (1971). GOSLINER & GRIFFITHS (1980) considered both of these genera as junior synonyms of *Flabellina* Voigt, 1834. This view has been widely accepted, and is further supported by GOSLINER & KUZIRIAN's recent (1990) cladistic analysis of the family.

The systematic status of *Flabellina rubrolineata* (O'Donoghue, 1929) has recently been revised by GOSLINER & KUZIRIAN (1990). Specimens identified by EV. MARCUS & ER. MARCUS (1961, 1970) from Brazil and the Gulf of California have been shown to represent a distinct species, *Flabellina marcusorum* Gosliner & Kuzirian, 1990, and *F. rubrolineata* is restricted to the Indo-Pacific tropics.

Flabellina rubrolineata is morphologically similar to specimens described by RISBEC (1928, 1953) from New Caledonia. In the discussion of *F. bicolor*, in the present work, difficulties with the systematic status of Risbec's *Coryphella ornata* were resolved. GOSLINER (1980) discussed the status of Risbec's "variété violacée" of *F. ornata*, noting that it appeared to be distinct from *F. ornata*. Its triseriate radula, with denticulate lateral teeth, clearly establish its placement within the genus *Flabellina*. RISBEC's (1928:pl. 9, fig. 6) description of the color of the violet variety of *F. ornata* indicates that the animal is rose violet with three longitudinal red lines. This pattern is identical to that described for *F. rubrolineata*. The rhinophores are described as perfoliate only on the posterior side with very long lamellae. We interpret this as meaning papillate rather than perfoliate rhinophores. The radular morphology of this variety of *F. ornata* (RISBEC, 1928:fig. 89, 3) is virtually identical to that depicted by BABA (1955:fig. 41c) for *F. rubrolineata*.

It is apparent that these two species are synonymous. However, the *International Code of Zoological Nomenclature* states that vernacular names have no systematic status. Thus, Risbec's 1928 taxon cannot have priority over *Coryphellina rubrolineata* O'Donoghue, 1929. It appears that *Coryphella ornata* var. *violacea* Risbec, 1953, constitutes a validly described subspecies. Nevertheless, it is here considered a junior subjective synonym of *Flabellina rubrolineata* (O'Donoghue, 1929) due to priority of publication.

Species of *Flabellina* with papillate rhinophores and a triaulic reproductive system are compared in Table 2.

Flabellina exoptata Gosliner & Willan,
sp. nov.

(Figures 1F, 18–20)

Distribution: This species has been found from Enewetak, Marshall Islands (Scott Johnson, personal communica-

Table 2

Morphological variation in *Flabellina* species with elongate papillae on rhinophores.

Species	Color	Ceratal arrangement	Radular formula	Denticles on either side of rachidian	Denticles on lateral	Receptaculum seminis	Bursa copulatrix	Vas deferens
<i>delicata</i>	body reddish purple, rhinophores red, cerata with opaque white & yellow & opaque white band	all arches	31 × 1.1.1	6-9	15-18	bilobed	reduced	short
<i>exoptata</i>	body pinkish-purple, rhinophores red with yellow spots, cerata with purple & white bands	preanal arch, postanal rows	23-37 × 1.1.1	7-10	13-20	bilobed	absent	short
<i>marcusorum</i> Gosliner & Kuzirian, 1990	body pink, cerata, rhinophores & oral tentacles purple & white	all arches	27-34 × 1.1.1	5-8	4-12	bilobed	well developed, stalked	elongate
<i>poenicia</i> (Burn, 1957)	body translucent white with red cerata, purple spots on head	all arches	34 × 1.1.1	6-7	4	—	—	—
<i>rubrolineata</i> (O'Donoghue, 1929)	body whitish or purple; 3 longitudinal red or purple lines	all arches	30-32 × 1.1.1	6-9	7-10	bilobed	reduced	short

tion), Guam (Clay Carlson and Patty Jo Hoff, personal communication), Fiji (present study), Queensland, Australia (present study), Western Australia (Neville Coleman, personal communication), Papua New Guinea (present study), Malaysia (Ho Soon Lin, personal communication), and Aldabra Atoll (present study).

Etymology: The epithet *exoptata* means "much desired" and refers to the strikingly beautiful color of this species.

Type material: Holotype, CASIZ 070988, Planet Rock, 10 km S of Madang, Papua New Guinea, 24.4 m (maximum) depth, 19 January 1988, T. M. Gosliner.

One paratype, CASIZ 070979, Passe Femme, Aldabra Atoll, Seychelles, 0.5 m depth, 12 March 1986, T. M. Gosliner. Eight paratypes, CASIZ 070980, 2 dissected, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. One paratype, CASIZ 070978, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. Two paratypes, USNM 859084, Passe Femme, Aldabra Atoll, Seychelles, 17 March 1986, T. M. Gosliner. One paratype, CASIZ 070981, dissected, Madang, Papua

New Guinea, 4 October 1986, J. Darr. Two paratypes, CASIZ 070982, N end Rasch Pass, Madang, Papua New Guinea, 18.3 m depth, 6 October 1986, T. M. Gosliner. One paratype, CASIZ 070983, lighthouse, Madang, Papua New Guinea, 18.3 m depth, 17 October 1986, M. T. Ghiselin. Two paratypes, CASIZ 070984, lighthouse, Madang, Papua New Guinea, 15.2 m depth, 21 October 1986, T. M. Gosliner. One paratype, CASIZ 070985, Anemone Reef, E of Riwo Island, Madang, Papua New Guinea, 13.7 m depth, 10 January 1988, T. M. Gosliner. One paratype, CASIZ 070986, lighthouse, Madang, Papua New Guinea, 33.5 m depth, 15 January 1988, T. M. Gosliner. Two paratypes, CASIZ 070987, the Blowhole, approximately 1 km S of Cape Croiselles, N of Madang, Papua New Guinea, 24.4 m depth, 18 January 1988, T. M. Gosliner. One paratype, AMS C164085, coral rubble, the Quarry, near Bunu Village, 30 km N of Madang, Papua New Guinea, 3-5 m depth, 21 January 1988, R. C. Willan. Two paratypes, CASIZ 070989, lighthouse, Madang, Papua New Guinea, 7.6 m average depth (27.4 m maximum), 22 January 1988, T. M. Gosliner. One paratype,

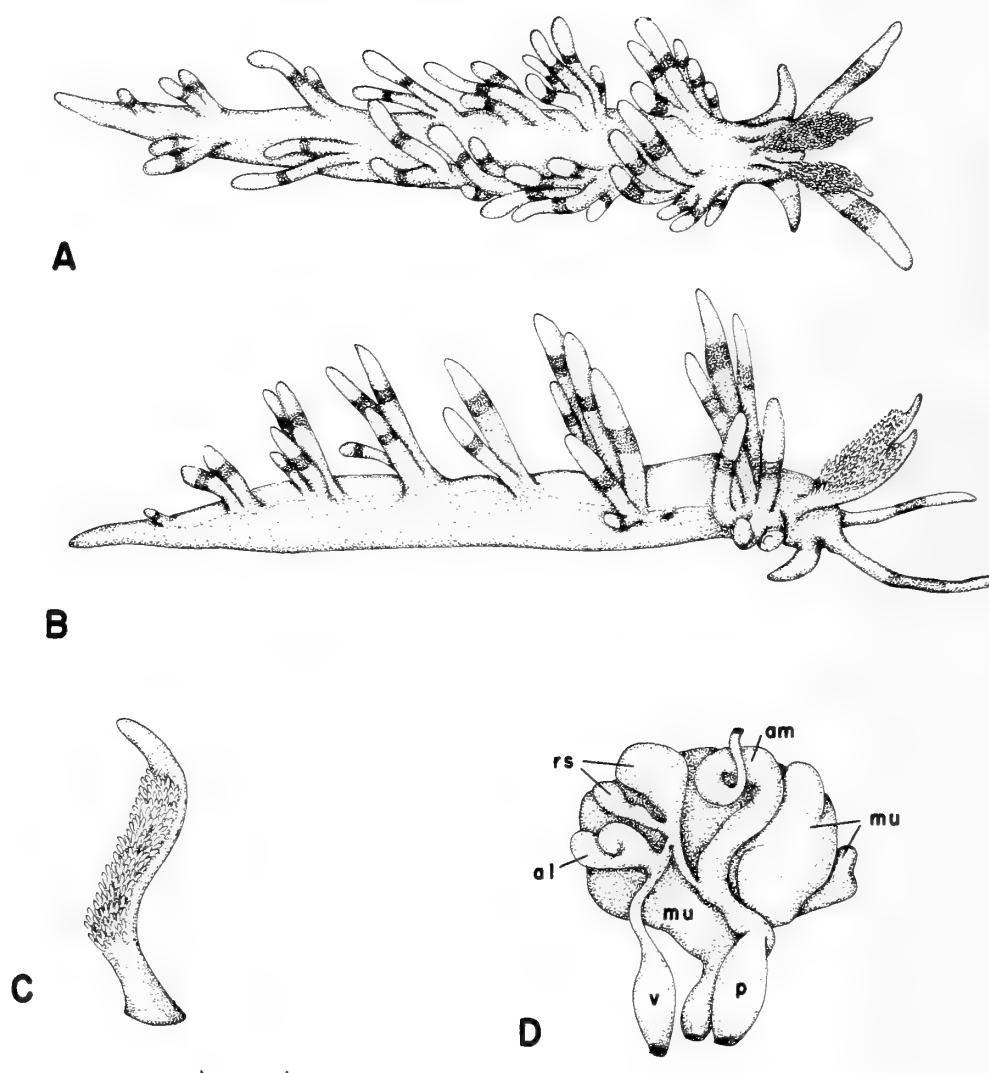


Figure 18

Flabellina exoptata Gosliner & Willan, sp. nov. A. Dorsal view of 21 mm living animal. B. Lateral view. C. Rhinophore, scale = 1.0 mm. D. Reproductive system: al, albumen gland; am, ampulla; mu, mucous gland; p, penis; rs, receptaculum seminis; v, vagina; scale = 0.5 mm.

CASIZ 060991, Barracuda Point, Pig Island, Madang, Papua New Guinea, 7.6 m depth, 7 February 1988, T. M. Gosliner. One paratype, AMS C164084, coral rubble, patch reef 1 km S Lian Island, 15 km SE of Port Moresby, Papua New Guinea, 10 m depth, D. J. Brunkhorst, 17 June 1988.

One paratype, CASIZ 070992, Barracuda Point, Pig Island, Madang, Papua New Guinea, 25 m depth, 16 July 1989, T. M. Gosliner.

One paratype, AMS C164083, feeding on *Halocordyle disticha*, on vertical wall of a bommie, "The Canyons," SE side of Heron Island, Capricornia Section, Great Barrier Reef, Queensland, Australia, 10 m depth, 20 August 1981, M. Ready.

External morphology: The living animals reach 30 mm in length. The general body color is deep pinkish purple. Basally, the oral tentacles are the same color as the rest of the body. Their middle third is deep purple and the outer third is generally opaque cream yellow. However, in some specimens from Aldabra Atoll, there is no opaque pigment on the outer portion of the tentacles and they are the same color as the rest of the body. Purple pigment is also present on the apical portion of the foot corners. The rhinophores are vivid orange with yellow pigment on the apices of the rhinophoral papillae. The basal half to two-thirds of the cerata is pinkish purple. Above this section, a deep purple ring is present. The apical portion of the cerata is opaque cream yellow.

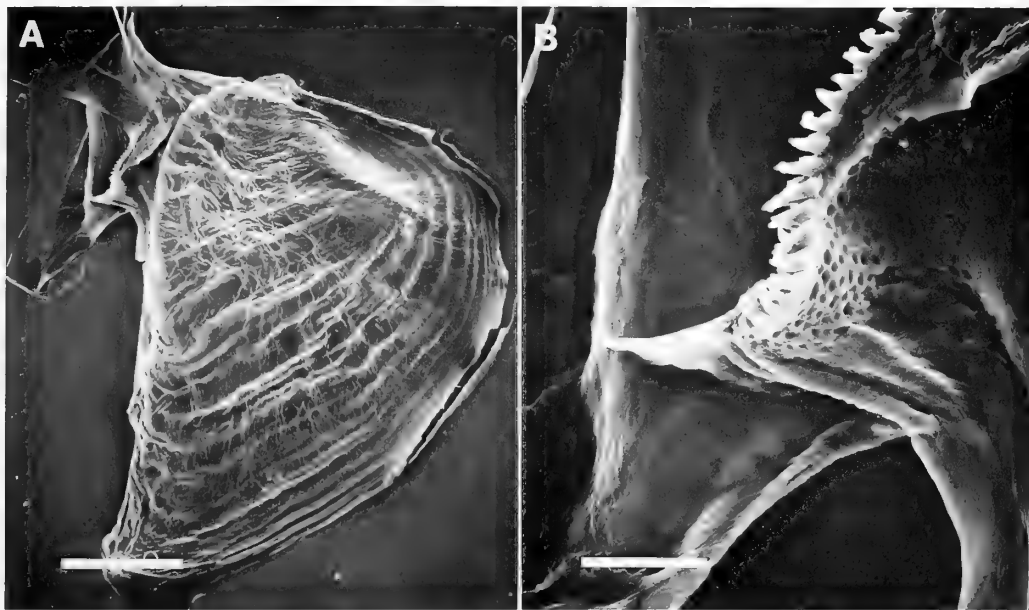


Figure 19

Flabellina exoptata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Jaw, Aldabra Atoll, scale = 200 μ m. B. Masticatory border, Aldabra Atoll, scale = 30 μ m.

The body is stockier than other members of the genus (Figure 18A). The notal brim is expanded at the level of each ceratal group, but is otherwise reduced compared to *Flabellina rubrolineata*. The oral tentacles are cylindrical throughout their length and they taper to an acute apex. The rhinophores (Figure 18B) are thick basally, and terminate in a distinctly pointed apex. The posterior side of each rhinophore bears over 120 densely packed, elongate papillae. The foot corners are elongate and tentacular, and are generally recurved posteriorly when the animal is actively crawling. The cerata are thick and cylindrical for most of their length, but taper to an acute apex. The cerata are slightly elevated from the notum on a common peduncle. The cerata are arranged in distinct rows. The precardiac ceratal cluster consists of three distinct rows, with 1–3 cerata per row. The postcardiac cerata are arranged in 4 or 5 linear rows that are well separated from each other. The anterior postcardiac row contains the most cerata (3–5). The more posterior rows contain fewer cerata, and the posteriormost row consists of only a single ceras. The gonopore is situated ventral to the second and third ceratal rows on the right side of the body. The pleuroproct anus is located below the notum within the interhepatic space. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The muscular buccal mass occupies the anterior portion of the body, from the rhinophores to the anterior end of the head. The narrow ducts of the paired oral glands emanate from the anterior end of the buccal mass. These glands are highly ramified and extend pos-

teriorly into the peduncle of the anteriormost ceratal cluster. The chitinous jaws (Figure 19A) are elongate and broad. The masticatory border (Figure 19B) bears several rows of elongate denticles. The denticles of the outermost row are longest.

The radular formula is $23-37 \times 1.1.1.$ in the two specimens examined. The rachidian teeth are narrow and elongate. The posterior limit of each limb bears a peduncle for attachment to the following tooth. The cutting edge of the teeth bears 7–10 elongate denticles on either side of the elongate, acutely pointed central cusp. The central cusp is depressed below the level of the adjacent denticles. The lateral teeth are triangular with a broad base and an elongate, acutely pointed primary cusp. There are 13–20 minute, acutely pointed denticles along the inner margin of the tooth.

Reproductive system (Figure 18D): The preampullary duct is narrow and elongate. It expands into an elongate, curved ampulla. The ampulla narrows again and divides into the oviduct and vas deferens. The oviduct is narrow and elongate and expands to join the two large receptacula seminis. The inner receptaculum is distinctly larger than the one closer to the female gland mass. The oviduct again narrows and enters the female gland mass near the small albumen gland. The albumen and membrane glands are much smaller than the mucous gland, which comprises the bulk of the reproductive system. The distinct vaginal duct continues from the oviduct to its own aperture, adjacent to the penis. The vagina is expanded for most of its distal portion, but a distinct bursa copulatrix is absent. The vas

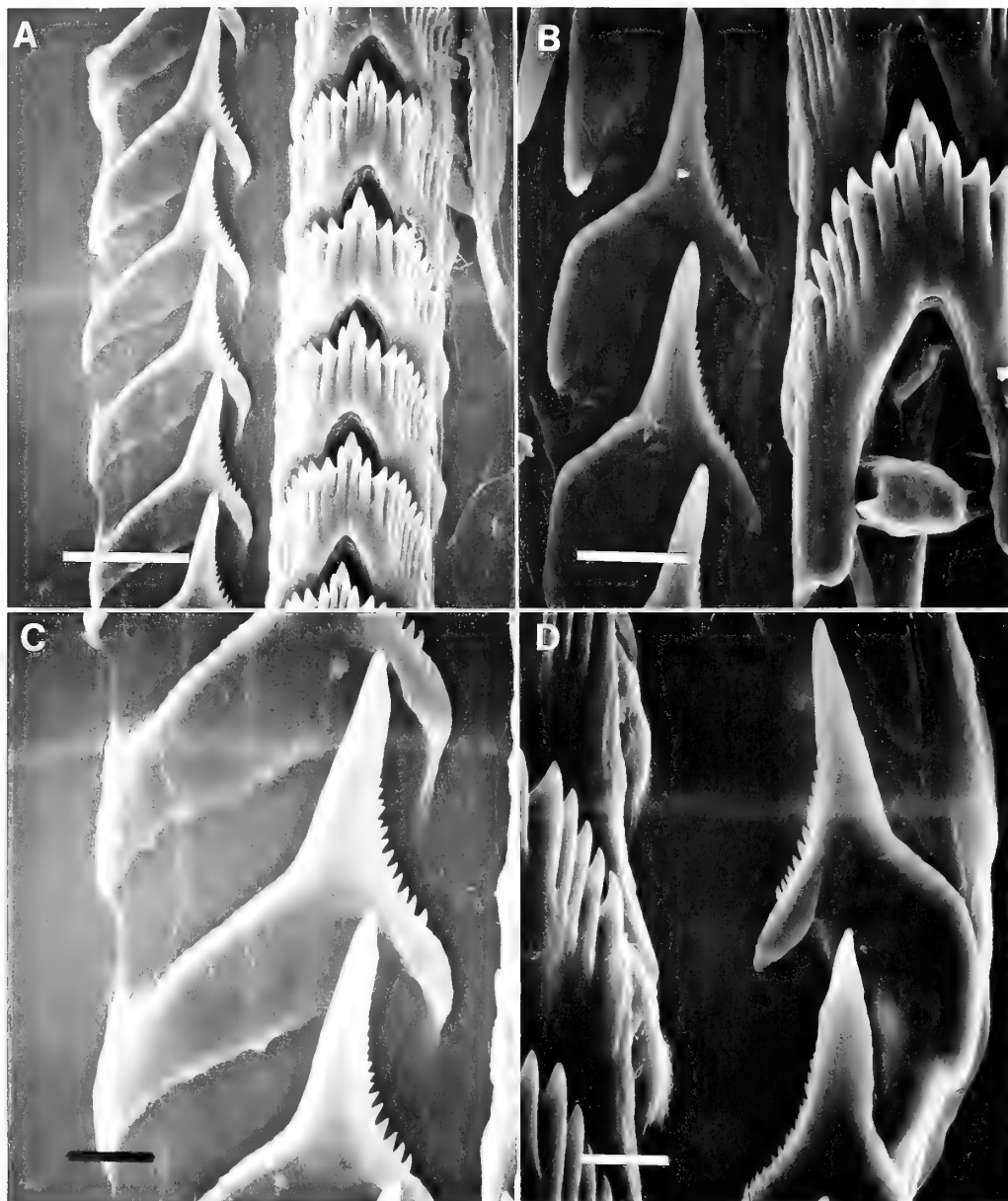


Figure 20

Flabellina exoptata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Rachidian and lateral teeth, Madang, Papua New Guinea, scale = 30 μm . B. Rachidian and lateral teeth, Aldabra Atoll, scale = 15 μm . C. Lateral teeth, Madang, Papua New Guinea, scale = 10 μm . D. Lateral teeth, Aldabra Atoll, scale = 10 μm .

deferens is short but expands into a small prostatic segment. The prostatic portion expands further into the broad penial sac containing the simple, unarmed penis.

Discussion: Its unique color pattern readily distinguishes *Flabellina exoptata* from three other described species of *Flabellina* with papillate rhinophores, *Flabellina rubrolineata*, *F. poenicia* (Burn, 1957), and *F. marcusorum* Gosliner & Kuzirian, 1990. All these species have the cerata of the

postcardiac groups arranged in horseshoe-shaped arches, whereas those of *F. exoptata* are in simple, linear rows.

In *Flabellina marcusorum*, the bursa copulatrix is large and obvious, whereas in *F. rubrolineata* and *F. delicata* it is reduced, and in *F. exoptata* it is entirely absent. The reproductive system of *F. poenicia* remains unknown. The vas deferens is shorter in *F. exoptata* than in *F. rubrolineata* and *F. marcusorum*.

In coloration, *Flabellina exoptata* is most similar to *F.*

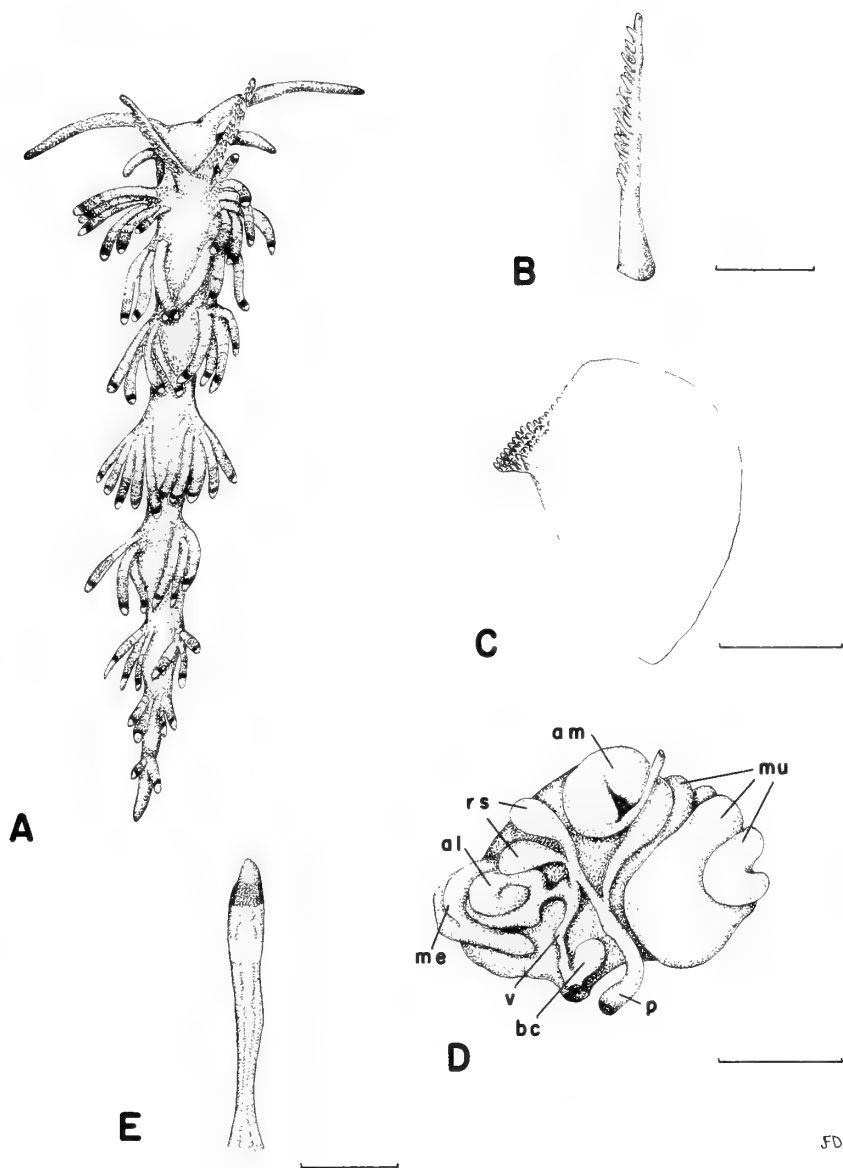


Figure 21

Flabellina delicata Gosliner & Willan, sp. nov. A. Dorsal view of 16 mm living animal. B. Rhinophore, scale = 1.0 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; p, penis; rs, receptaculum seminis; v, vagina, scale = 1.0 mm. E. Ceras, scale = 1.0 mm.

marcusorum, but this species lacks the yellow pigment on the posterior surface of the rhinophoral papillae, which is present in *F. exoptata*. In addition, *F. marcusorum* has opaque white pigment on the posterior end of the foot, which is not present in *F. exoptata*.

This species has been erroneously identified as *Flabellina macassarana* Bergh, 1905, on a Malaysian postage stamp. However, *F. macassarana* differs from *F. exoptata* in several important aspects. The color of *F. macassarana* is pinkish yellow without the striking purple and yellowish bands that distinguish *F. exoptata*. Also, *F. macassarana*

has perfoliate rather than papillate rhinophores. The shape and denticulation of the radular teeth differ markedly between the two species. *Flabellina macassarana* has only 20 rows of teeth in the radula, whereas *F. exoptata* has 23–37 rows. Both the rachidian and lateral teeth of *F. macassarana* have far fewer denticles than do the teeth of *F. exoptata*. Therefore, *F. exoptata* can be clearly distinguished from *F. macassarana*. *Flabellina macassarana* is known only from Bergh's original description and the unique holotype could not be located in the in the Zoologisch Museum, Amsterdam (R. Moolenbeek, personal

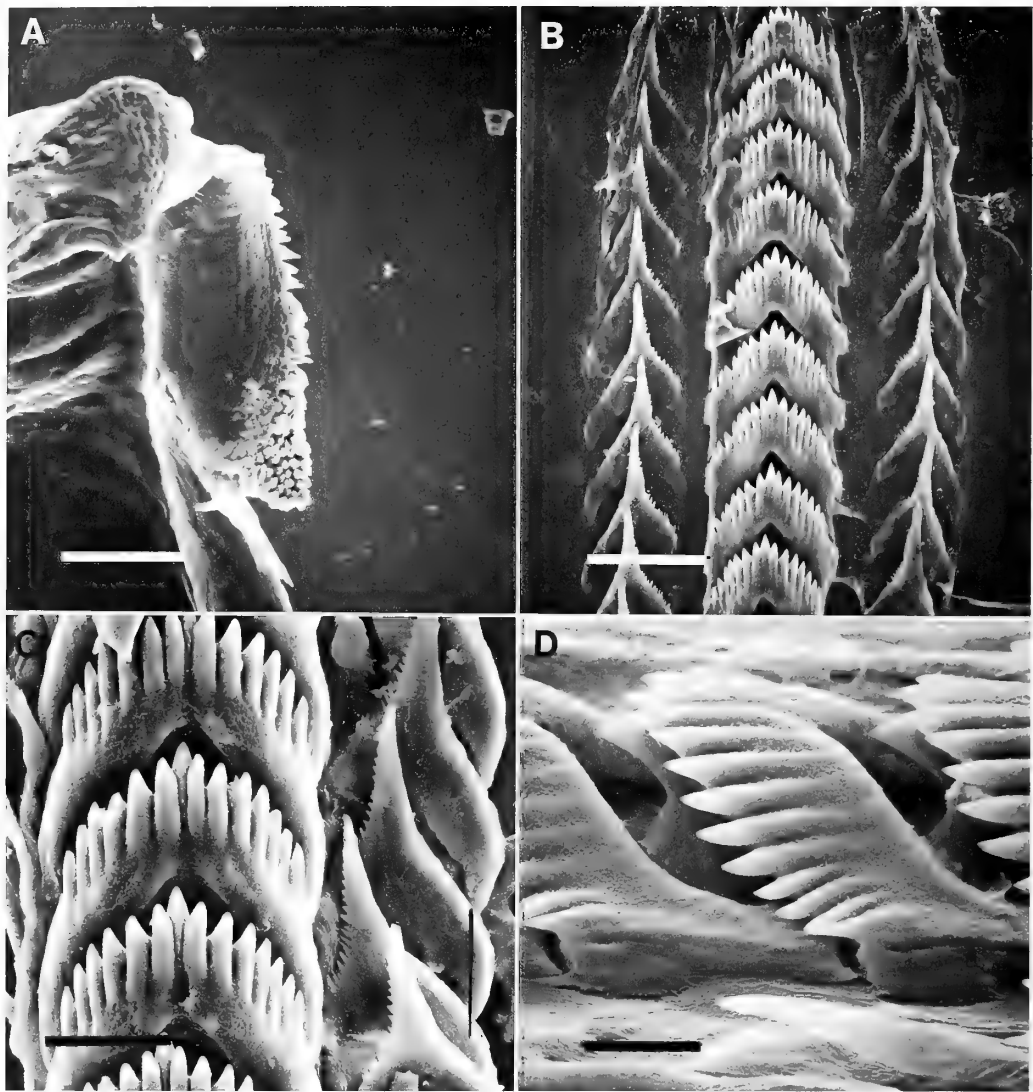


Figure 22

Flabellina delicata Gosliner & Willan, sp. nov., scanning electron micrographs. A. Masticatory border, Madang, Papua New Guinea, scale = 40 μ m. B. Entire width of radula of holotype, Madang, Papua New Guinea, scale = 40 μ m. C. Entire width of radula, Aliwal Shoals, South Africa, scale = 20 μ m. D. Lateral view of rachidian teeth of holotype, Madang, Papua New Guinea, scale = 10 μ m.

communication). Determination of its relationship to other members of the genus requires further study and elaboration of the original description.

Flabellina delicata Gosliner & Willan,
sp. nov.

(Figures 1G, 21–23)

Coryphellina sp.: GOSLINER, 1987:114, fig. 224.

Distribution: *Flabellina delicata* is known from Papua New Guinea (present study) and from Natal, South Africa (GOSLINER, 1987, and present study).

Etymology: The epithet *delicata* refers to the elongate, graceful body form of this species.

Type material: Holotype: California Academy of Sciences, CASIZ 070999, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 30.5 m (maximum) depth, 11 February 1988, T. M. Gosliner.

Paratypes: One specimen, CASIZ 071000, the Quarry, approximately 1 km S of Cape Croiselles, Madang, Papua New Guinea, 10.4 m depth, 19 February 1988, T. M. Gosliner. One specimen, South African Museum, Cape Town, SAM A35719, dissected, Aliwal Shoals, off Scottburgh, Natal, South Africa, 12.2 m depth, 2 May 1982, T. M. Gosliner.

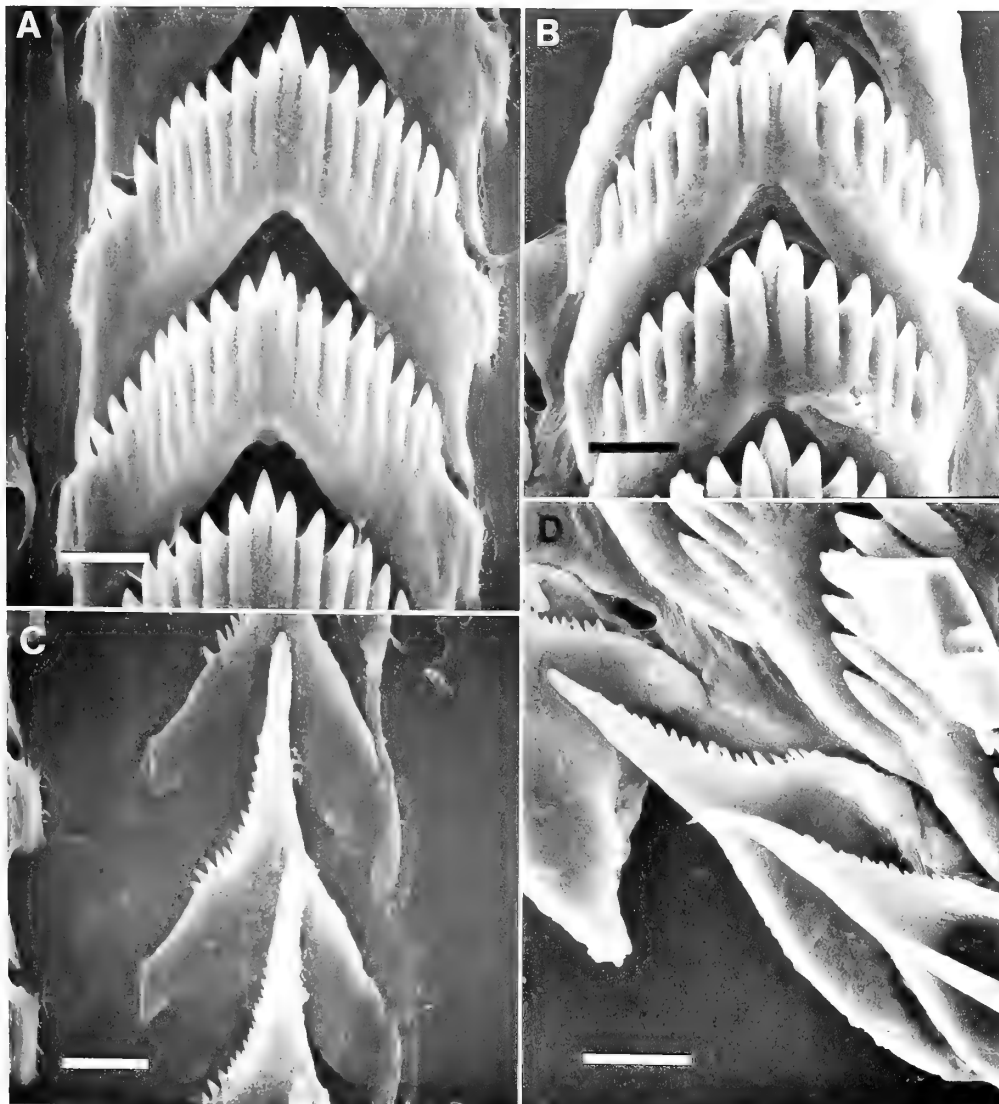


Figure 23

Flabellina delicata Gosliner & Willan, sp. nov., scanning electron micrographs, scales = 10 μ m. A. Dorsal view of rachidian teeth of holotype, Madang, Papua New Guinea. B. Dorsal view of rachidian teeth, Aliwal Shoals, South Africa. C. Lateral teeth of holotype, Madang, Papua New Guinea. D. Lateral teeth, Aliwal Shoals, South Africa.

External morphology: The living animals (Figure 1G) are 15–20 mm in length. The general body color is deep reddish purple. Generally, the oral tentacles are a deeper purple than the rest of the body. The rhinophores are deep red throughout. The cerata are translucent white basally, with the opaque white digestive gland giving the cerata an overall white appearance. Near the middle of each ceras, an opaque white transverse band is present on its surface. More distally, the ceras is again translucent and a golden-yellow-orange enlarged portion of the digestive gland is visible. A subapical transverse ring of translucent purple is present just below the translucent white apex.

The body is narrow and delicate in appearance (Figure

21A). The notal brim is slightly expanded at the base of the cerata, but is otherwise reduced. The oral tentacles are slender and elongate, terminating at an acute apex. The rhinophores (Figure 21B) are elongate and slender with approximately 30 well-separated papillae on their posterior surface. The rhinophores terminate at an acute apex. The tentacular foot corners are elongate and acutely pointed. The numerous cerata are slender and cylindrical throughout their length (Figure 21E). The cerata are arranged in distinct, well-separated clusters. The precardiac cluster contains 3 or 4 distinct rows with 1–6 cerata per row. The postcardiac clusters are arranged in 5–8 horse-shoe-shaped arches. The anteriormost arch contains 6–10

Table 3.

Morphological variation in *Flabellina*. 0 = ancestral; 1–3 = derived states; 9 = missing data.

Species	ceratal peduncles	preanal cerata	rhino- phores	anus	oral glands	central cusp	receptac- ulum seminis	bursa copulatrix	foot corners	repro- ductive system
ancestor	1	0	0	2	1	2	0	0	1	0
<i>affinis</i>	2	0	1	2	1	2	1	0	1	0
<i>albomarginata</i>	1	0	2	2	1	2	0	2	1	0
<i>babai</i>	2	1	1	2	1	2	0	2	1	0
<i>baetica</i>	1	0	2	2	1	2	0	2	1	0
<i>bertschi</i>	1	0	0	2	1	2	0	2	1	0
<i>bicolor</i>	2	2	1	2	1	3	1	0	1	0
<i>bilas</i>	2	2	1	2	1	2	1	1	1	0
<i>delicata</i>	1	0	2	2	1	2	0	1	1	1
<i>engeli</i>	2	1	1	2	1	2	0	2	1	0
<i>exoptata</i>	1	0	2	2	1	2	0	2	1	1
<i>funeka</i>	2	0	1	2	1	2	0	0	1	0
<i>ischitana</i>	2	0	1	2	1	9	0	0	1	0
<i>marcusorum</i>	1	0	2	2	1	2	0	0	1	1
<i>pedata</i>	1	0	0	2	1	2	0	2	1	0
<i>pellucida</i>	1	0	0	2	1	2	0	0	1	0
<i>poenicia</i>	1	0	2	2	1	2	9	9	1	9
<i>rivo</i>	2	2	1	2	1	3	2	1	1	0
<i>rubrolineata</i>	1	0	2	2	1	2	0	1	1	1
<i>rubropurpurata</i>	2	0	1	2	1	2	0	0	1	0
<i>telja</i>	2	0	1	2	1	2	0	0	1	0
character number	1	2	3	4	5	6	7	8	9	10

cerata. More posterior arches contain fewer cerata. The posteriormost arch contains 1–3 cerata. The gonopore is situated ventral to the posterior 2 rows of the precardiac ceratal cluster. The pleuroproct anus is situated in the interhepatic space, ventral to the edge of the notum. The nephroproct is immediately anterodorsal to the anus.

Buccal mass: The buccal mass is small relative to the rest of the body. The narrow ducts of the paired oral glands emanate from the anterior portion of the buccal mass. The jaws (Figure 21C) are broad and ovoid. The masticatory border (Figure 22A) bears 5 or 6 rows of small denticles. The outermost row bears the longest denticles.

The radular formula is $31 \times 1 \cdot 1 \cdot 1 \cdot$ in two specimens examined. The rachidian teeth (Figures 22B–D, 23A, B) are broad with short lateral limbs. There are 6–9 elongate, acute denticles on either side of the elongate central cusp. The central cusp is depressed below the level of the adjacent denticles (Figure 22D). The lateral teeth (Figure 23C, D) are triangular with a relatively broad base. The primary cusp is narrow and elongate. There are 15–18 minute denticles along most of the inner margin of the laterals.

Reproductive system (Figure 21D): The narrow preampullary duct curves and widens into the saccate ampulla. The ampulla curves, narrows, and divides into the oviduct and vas deferens. The short oviduct joins with the two receptacula seminis, which are approximately equal in size. The oviduct continues for a short distance and enters

the albumen gland. The albumen and membrane glands are adjacent to each other and are much smaller than the voluminous mucous gland. From the entrance of the oviduct into the female gland mass, the vaginal duct continues distally towards its own aperture adjacent to the penis. The vagina gives rise to a small bursa copularix immediately prior to exiting at the vaginal pore. The vas deferens is short and straight and appears to be prostatic nearest the ampulla. It is uniform in diameter for most of its length and is contiguous with the simple, unarmed penial papilla.

Discussion: By means of its unique color pattern, *Flabellina delicata* can be distinguished from other members of the genus with papillate rhinophores. Its notal brim is more reduced than *F. rubrolineata*, as in *F. marcusorum* and *F. exoptata*. The papillae on the rhinophores are fewer in number and sparser in arrangement than in the other species that possess papillae. The postcardiac ceratal clusters are arranged in horseshoe-shaped arches as in *F. rubrolineata* and *F. marcusorum* rather than in linear rows as in *F. exoptata*. However, *F. delicata* has more cerata per cluster than do the other species.

The rachidian radular teeth of *Flabellina delicata* are broader relative to their length than in *F. rubrolineata*, *F. marcusorum*, or *F. exoptata*. Only *F. exoptata* and *F. delicata* have numerous denticles on the cutting edge of the lateral teeth.

The reproductive system of *Flabellina delicata* is most similar to *F. rubrolineata*. Both species have a reduced bursa

Table 3
Continued.

lateral teeth	number of laterals	rhino- phoral papillae	ceratal groups	rhino- phores	penial warts	denticles on lateral	notal brim	prostate	anterior liver arch	receptac- ulum seminis
0	1	0	0	0	0	0	0	0	0	0
0	1	0	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	0	0	1
0	1	0	0	2	0	0	1	0	0	0
1	1	1	0	0	0	0	0	0	1	0
0	1	0	0	0	0	0	0	0	0	1
0	1	0	0	2	0	0	1	0	0	0
0	1	0	0	2	0	0	1	0	0	0
0	1	2	0	0	0	1	1	0	1	1
0	1	0	0	2	0	0	1	0	0	0
0	1	2	1	0	0	1	1	0	1	1
0	1	0	0	1	0	0	1	1	0	0
1	1	0	0	1	0	0	1	1	0	0
0	1	2	0	0	0	0	1	0	1	1
0	1	0	0	0	0	0	0	0	0	1
1	1	0	0	0	0	0	0	0	0	0
0	1	2	0	0	0	0	0	0	1	9
0	1	0	0	2	0	0	1	0	0	0
0	1	2	0	0	0	0	0	0	1	1
0	1	0	0	2	0	0	1	0	0	0
0	1	0	0	2	1	0	1	0	0	0
11	12	13	14	15	16	17	18	19	20	21

copulatrix. However, the vas deferens is shorter and straighter in *F. delicata* than in *F. rubrolineata*.

Three other distinct species have sparsely papillate rhinophores, *Flabellina albomarginata* Miller, 1971, *F. baetica* Garcia Gomez, 1984, and *Flabellina* sp. 1 (GOSLINER, 1987). These species differ from the above-mentioned taxa in several significant regards. The papillae on the rhinophores are less well developed, the cerata are arranged in simple crowded rows (except in *F. baetica*), and the reproductive system is diaulic rather than triaulic.

DISCUSSION

The phylogenetic and systematic relationships of the Flabellinidae have recently been examined by GOSLINER & KUZIRIAN (1990). From their analysis, it is apparent that the genus *Flabellina* contains numerous, morphologically diverse species. Included in the genus are some of the most primitive aeolids, such as *F. islandica* (Odhner, 1937), as well as intermediate and highly derived taxa. They concluded that the most highly derived taxa formed two distinct clades. All of the taxa included in the present study are members of these two clades. In members of both of these clades, digitate oral glands and a depressed central cusp of the rachidian tooth are present. The first of these clades includes taxa with cerata elevated on distinct peduncles and densely annulate or perfoliate rhinophores. The second clade contains taxa with a bilobed receptacu-

lum seminis, and most members of this clade also possess papillae ornamenting the posterior face of the rhinophores.

In order to examine further the phylogeny of members of these two clades of derived flabellinids, the morphology of the taxa described here was examined and the morphology of previously described flabellinids was reviewed and, in several cases, re-examined. Eight additional characters, not included in the previous study, were examined here. These data are compiled in Table 3.

Character Polarity

Twenty-one characters of 20 taxa were included. The polarity of these characters was determined using outgroup comparison of less derived flabellinids (see GOSLINER & KUZIRIAN, 1990). The basis for determining polarity of these features is discussed below. The sequence of characters is identical to that presented in Tables 3 and 4.

1. Ceratal peduncles: Outgroups of flabellinids and species of *Notaeolidia* have the cerata arranged in linear rows. These rows emerge from epithelial tissue that is at the same level as the rest of the notum. In more derived taxa, the ceratal clusters emerge from stalked clusters, which are well elevated from the notum. These may contain compound ceratal clusters or simple ones.

2. Preanal ceratal rows: Species of less derived flabellinids, including all of the taxa not included in this study (outgroup taxa), have several rows of cerata anterior to

Table 4
Coding for characters in Table 3.

1. ceratal peduncles	1 = low	2 = elevated	
2. preanal cerata	0 = 3–4 rows	1 = 2 rows	2 = one row
3. rhinophores	0 = simple	1 = ringed	2 = papillate
4. anus	1 = posterior	2 = interhepatic	
5. oral glands	0 = absent	1 = present	
6. central cusp	2 = depressed	3 = elevated	
7. receptaculum seminis	0 = semiserial	1 = serial	2 = absent
8. bursa copulatrix	0 = stalked	1 = reduced	2 = absent
9. foot corners	0 = rounded	1 = tentacular	
10. reproductive system	0 = diaulic	1 = triaulic	
11. lateral teeth	0 = denticulate	1 = smooth	
12. number of laterals	0 = more than 1	1 = 1	
13. rhinophoral papillae	0 = short	1 = elongate	
14. ceratal groups	0 = all arches	1 = posterior rows	
15. rhinophores	0 = no rings	1 = annulate	2 = perfoliate
16. penial warts	0 = absent	1 = present	
17. lateral denticles	0 = few	1 = many	
18. notal brim	0 = present	0 = absent	
19. prostate	0 = uniform	1 = constricted	
20. anterior liver arch	0 = absent	1 = present	
21. receptaculum seminis	0 = single	1 = bilobed	

the anus, which form a distinct ceratal cluster. In some derived species that have cerata elevated on peduncles, the number of anterior ceratal rows is reduced. In the most highly derived species (e.g., *Flabellina bicolor*, *F. riwo*, and *F. bilas*), there is only a single ceratal row per peduncle in both the preanal and postanal ceratal clusters.

3. Rhinophores: In most ancestral flabellinids the rhinophores are simple, without any ornamentation. GOSLINER & KUZIRIAN (1990) have shown that this appears to be the case in the least derived members of the family. Ornamented rhinophores have evolved independently within different lineages of the family. Within the more highly derived members of the family studied here the rhinophores may be simple, ringed (annulate or perfoliate), or papillate. The simple condition is considered to represent the ancestral state. Ringed and papillate rhinophores have probably both evolved directly from simple ones, though the sequence of changes is uncertain. Owing to the lack of certainty of the evolutionary sequence of derived states, this character is treated as unordered in the present analysis.

4. Anus: In the Notaeolidiidae and less derived members of the Flabellinidae, the anus is situated in the pleuroproctic position, and is located in the posterior half of the body. In more derived taxa, the anus is situated near the middle of the most anterior postanal ceratal cluster. In all of the taxa examined here, the anus is situated within the interhepatic space, which represents the most derived condition within the family.

5. Oral glands: GOSLINER & KUZIRIAN (1990) suggested that an absence of oral glands represents the ancestral state

within the Flabellinidae, because oral glands are also absent in the Notaeolidiidae. Most primitive members of the Flabellinidae lack oral glands, with the exception of *Flabellina salmonacea* (Couthoy, 1838), which has a pair of ventral pyriform oral glands. In all of the taxa studied here, the oral glands are highly ramified, are found dorsally, and extend to the bases of the preanal ceratal cluster. Even in cases where the glands were not specifically described, such as in *Flabellina ischitana* Hirano & Thompson, 1990, they are evident in photographs of the living animal (HIRANO & THOMPSON, 1990:fig. 1).

6. Central cusp of the rachidian teeth: All of the less derived members of the Flabellinidae possess rachidian teeth of the radula with a central cusp that is above, or at the same level as, the adjacent denticles. This feature is especially evident when the teeth are viewed laterally. In almost all derived species, the central cusp is depressed below the level of the adjacent denticles. In two species examined in this study, *Flabellina riwo* and *F. bicolor*, the central cusp is elevated. This is considered to be a secondarily derived reversal of the depressed cusp within the in-group studied here. This assumption is based upon the highly derived nature of all other aspects of the morphology of these species.

7. Receptaculum seminis: EDMUNDS (1970) described two forms of the receptaculum seminis in aeolid nudibranchs. A serial arrangement has two distinct ducts entering the receptaculum, while a semiserial configuration has only a single duct entering the receptaculum. Edmunds considered the former to be the ancestral condition within the aeolids. This appears to be the case in *Notaeolidia*

(WÄGELE, in press), and was considered to represent the ancestral condition within the Flabellinidae (GOSLINER & KUZIRIAN, 1990). The majority of more derived species of flabellinids have a semiserial receptaculum. Some of the derived members studied here also possess a serial receptaculum. This is considered to be a secondarily derived reversal to a serial receptaculum from a semiserial condition. In one instance, in *Flabellina riwo*, the receptaculum is entirely absent. This is considered to be a further modification of the secondarily derived serial configuration.

8. Bursa copulatrix: The presence of a stalked bursa is considered to represent the ancestral state in the Aeolidacea (EDMUNDS, 1970). This plesiomorphic condition exists in the majority of the Flabellinidae (GOSLINER & KUZIRIAN, 1990). In other taxa, the bursa may be reduced in size and sessile, or it may be entirely absent. Both of these arrangements are considered derivations of the primitive state. It is difficult to place the derived states in a linear configuration, because loss of the bursa may not require reducing the bursa prior to loss. For this reason this character is treated as unordered.

9. Foot corners: A simply rounded anterior end of the foot is present in *Notaeolidia* (WÄGELE, in press) and in two primitive species of *Flabellina* (GOSLINER & KUZIRIAN, 1990), *F. islandica* and *F. salmonacea*. Possession of tentacular foot corners represents a derived state within the Flabellinidae. This apomorphic condition is present in all of the taxa examined in this study.

10. Reproductive system: GHISELIN (1966) argued that, in opisthobranchs, an androdiaulic reproductive system preceded a triaulic arrangement of organs. The vast majority of flabellinids have an androdiaulic reproductive system. However, a few species, which are highly apomorphic in other aspects of their anatomy, have a triaulic arrangement of reproductive organs. This is considered to represent an apomorphic feature within the flabellinids, and appears to be the case throughout the Opisthobranchia.

11. Lateral teeth: In species of *Notaeolidia* (WÄGELE, in press) and in most species of *Flabellina*, the lateral radular teeth bear a series of denticles along their inner edge. In a few species of *Flabellina* studied here, the laterals are smooth and entirely devoid of denticles. In *F. ischitana*, a few reduced denticles may be present or entirely lacking in different individuals (HIRANO & THOMPSON, 1990). The absence of denticles on the lateral teeth is considered to represent a derived feature within *Flabellina*.

12. Number of lateral teeth: In species of *Notaeolidia* (WÄGELE, in press) there is a variable number (3–5) of lateral radular teeth on either side of the rachidian. In *Flabellina islandica* there are two rows of laterals on either side of the rachidian. In the remainder of *Flabellina* species, there is only a single lateral tooth on either side of the rachidian. This is considered the derived state within the genus.

13. Rhinophoral papillae: In some species of Flabellinidae, Facelinidae, and Aeolidiidae, the posterior surface of the rhinophores bears numerous papillae. It is clear that this condition has arisen independently within these lineages of aeolids and represents a derived feature within each of these families. Within the Flabellinidae, some taxa have simple rounded papillae while others have elongate digitiform ones. On a functional basis, more elongate papillae probably arose from simply rounded ones. The derived condition provides greater surface area for chemosensory reception.

14. Ceratal groups: In a few species of flabellinids, the cerata are arranged in horseshoe-shaped arches, in a fashion similar to that described for the Favorininae (see EDMUNDS, 1970). A reduction of the postanal arches to linear rows represents a derived condition found only in *Flabellina exoptata*.

15. Rhinophoral rings: Most opisthobranchs utilize their rhinophores as their primary chemosensory organs. The Flabellinidae and other aeolidacean taxa include species with smooth and ornamented rhinophores. Smooth rhinophores provide less sensory surface area and are considered to represent the ancestral condition, based on functional criteria. The least derived members of Flabellinidae, Eubranchidae, Tergipedidae, and Aeolidiidae have smooth rhinophores. In derived species, the rhinophores are generally ornamented with either papillae (see above), well separated annulations or densely packed lamellae (perfoliate rhinophores). All of these conditions exist within the Flabellinidae. Judging from the cladogram presented by GOSLINER & KUZIRIAN (1990), it appears that annulate rhinophores originated several times within the family. Perfoliate rhinophores are present only in members of one of the most highly derived clades, that which includes *Flabellina bicolor* and its relatives (Table 1). The sister group of this clade includes *F. affinis*, and contains taxa with annulate rhinophores. The ancestors to these two clades had smooth rhinophores. It is clear that, within the Flabellinidae, both the annulate and perfoliate states are derived, but it is uncertain as to whether either condition is derived from the other. Functional arguments would suggest that perfoliate rhinophores would provide greater surface area than do annulate ones. From this perspective, it is hypothesized that perfoliate rhinophores are derived from annulate ones.

16. Penial papillae: Among members of the Flabellinidae, the presence of wartlike papillae on the penial papilla is limited to *Flabellina telja*. This state is not known in aeolidacean out-groups of flabellinids and represents a derived condition.

17. Denticles on lateral teeth: As discussed above, the taxa studied here include species with denticulate and smooth lateral teeth, and it has been concluded that denticulate teeth represent the ancestral condition. Two species of flabellinids with papillate rhinophores, *Flabellina*

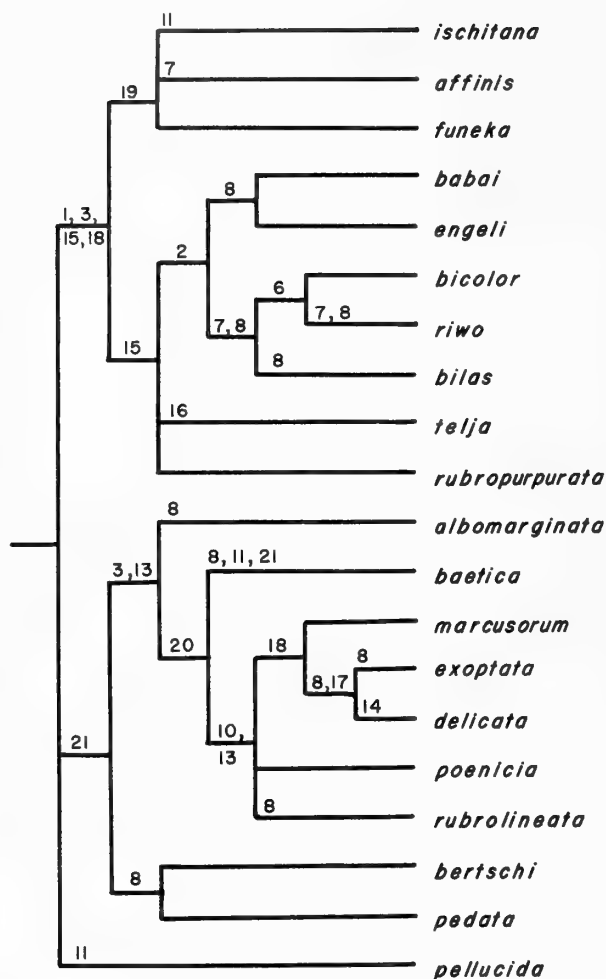


Figure 24

Cladogram depicting phylogeny of highly derived flabellinids included in this study.

exoptata and *F. delicata*, have more numerous denticles than other members of their clade or than in out-groups of flabellinids. Therefore, lateral teeth with multiple denticles are considered derived from teeth with few denticles.

18. Notal brim: The presence of a distinct rim of tissue along the dorsolateral margins of the body has been considered as a plesiomorphic feature within the Aeolidacea (ODHNER, 1939). In the least derived flabellinids, a continuous notal brim is present. In more derived flabellinids, the notal brim is interrupted, and in the most derived taxa the brim is entirely absent. In the clade of flabellinids studied here, the notal brim is either partially or entirely reduced. The latter is considered derived within the in-group.

19. Prostate: In almost all flabellinids, the prostate is of uniform diameter throughout its length. In *Flabellina af-*

finis, *F. funeka*, and *F. ischitana*, there is a constriction of the prostate near its distal end. This is considered a derived feature within this clade.

20. Anterior liver arch: In primitive members of the Flabellinidae and other aeolids, the cerata are arranged in simple linear rows. In a few derived flabellinids, the rows of cerata are elevated on a cushion that forms an arch-shaped expansion. This represents a derived state. As noted above, in *Flabellina exoptata* the postanal arches are secondarily reduced to form single linear rows.

21. Receptaculum seminis: In most species of flabellinids, the receptaculum seminis is a semiserial structure consisting of a single spherical or pyriform sac (see character 7 above). In some species studied here, the receptaculum consists of two distinct lobes. A bilobed receptaculum is considered to represent the apomorphic state.

In order to examine further the phylogeny of the taxa studied here, these morphological data were analyzed using PAUP (Phylogenetic Analysis Using Parsimony version 2.41 by David Swofford). All characters were treated as ordered, with the exceptions of the ornamentation of the rhinophores and the elaboration of the bursa copulatrix. The phylogeny of these highly derived Flabellinidae is presented here (Figure 24).

GOSLINER & KUZIRIAN (1990) argued that the cladogram they presented had implications for the systematics of the Flabellinidae. Exclusion of *Flabellina* and *Coryphellina* from *Coryphella* as distinct genera rendered *Coryphella* a paraphyletic taxon. Paraphyletic taxa are untenable in modern phylogenetic classification. Therefore, all species were contained within the single genus *Flabellina* on the basis of priority. The present analysis demonstrates that maintenance of the traditionally accepted confines of *Coryphella* makes the genus polyphyletic as well as paraphyletic.

The cladogram presented here is one of two most parsimonious cladograms. The other cladogram contains *Flabellina riwo* and *F. bilas* as sister taxa. These two taxa are the sister taxon of *F. bicolor*. The alternative hypothesis presented in Figure 24 was chosen since it required only one transformation of the depressed central cusp of the rachidian tooth to an elevated one. Instead, we hypothesize that the reduction of the bursa copulatrix occurred twice in these three taxa. The bursa copulatrix has been known to be reduced or lost in several other lineages.

Several unresolved trichotomies are presented. Further examination of the highly derived flabellinids studied here and the inclusion of other undescribed taxa may facilitate the revision of the phylogenetic hypotheses presented.

GOSLINER & KUZIRIAN (1990) noted that there is a distinct correlation between the phylogeny and biogeography of the Flabellinidae. Virtually all of the plesiomorphic taxa are found in polar or cold temperate oceans. More derived taxa are generally found in temperate wa-

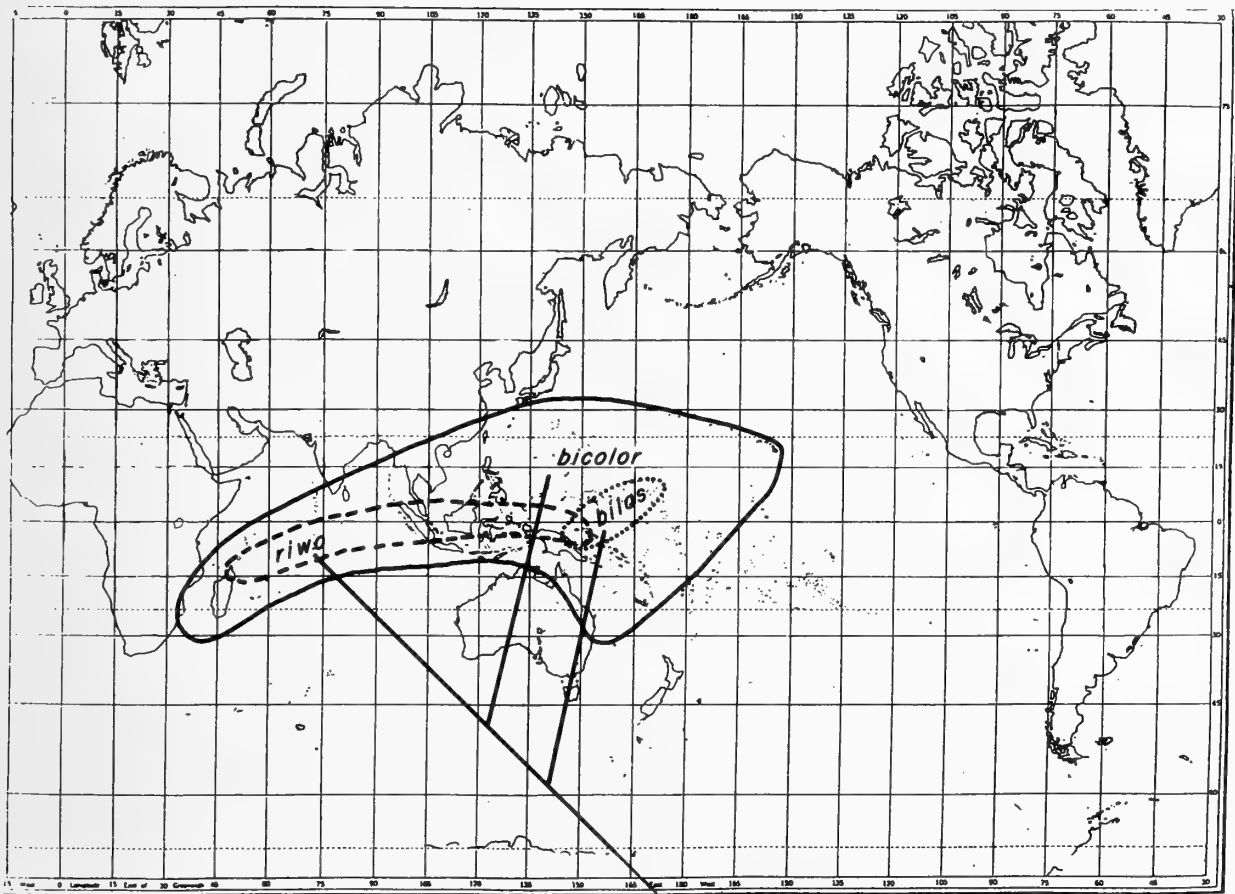


Figure 25

Area cladogram of one clade of flabellinids with perfoliate rhinophores.

ters, and the most derived taxa inhabit subtropical and tropical oceans. Area cladograms are presented for two of the clades studied here (Figures 25, 26). Neither of these examples demonstrates marked geographical separation or vicariance. Subsequent dispersal has swamped the original allopatric distributions at the time of speciation, and many of the species are presently sympatric over much of their ranges. In the one case where vicariance is clearly demonstrable, the separation of *Flabellina marcusorum* populations on either side of the Isthmus of Panama, no discernible morphological differentiation has occurred between allopatric populations (GOSLINER & KUZIRIAN, 1990), despite the fact that they have been separated for approximately 1.6 million years (WOODRING, 1966; ROSEN, 1976).

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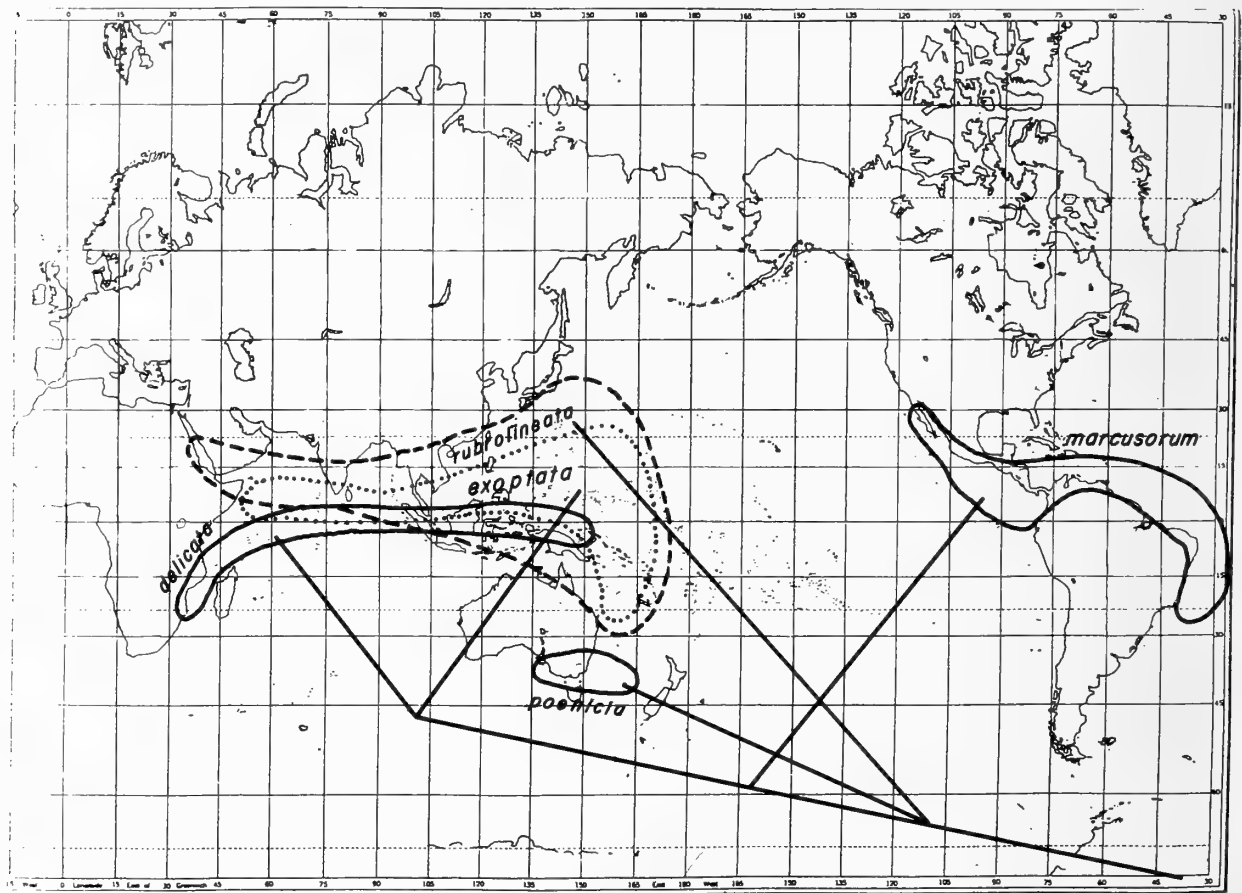


Figure 26

Area cladogram of flabellinids with triallic reproductive system and papillate rhinophores.

Lisa Borok printed the scanning electron micrographs, Pat Dal Porto prepared several tables, and Jean De-Mouthe prepared all the final pen and ink illustrations. We are especially grateful for their help.

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Nudibranch Spermatozoa: Comparative Ultrastructure and Systematic Importance

by

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Abstract. Spermatozoan ultrastructure is described for 27 nudibranch gastropods selected from both suborders (Anthobranchia, Cladobranchia) and all four superfamilies (Doridoidea, Dendronotoidea, Arminoidea, Aeolidoidea). Like most heterobranchs, nudibranchs possess complex spermatozoa characterized by distinctive acrosomal features (apical vesicle plus pedestal) and a highly modified mitochondrial derivative (paracrystalline and matrix components enveloping an axoneme and glycogen-filled helical compartment). Although no sperm autapomorphy defining the Nudibranchia could be found, sperm morphology offers many useful indicators of relationships between and within superfamilies. Four groups within the Doridoidea can be distinguished based on acrosomal and nuclear features: (1) Dorididae (*Jorunna*, *Rostanga*, *Doriopsis*, *Hypselodoris*), Chromodorididae (*Chromodoris*); (2) Dorididae (*Doris*, *Sclerodoris*, *Asteronotus*), Hexabranchidae (*Hexabranchus*); (3) Polyceridae (*Kaloplocamus*), Gymnodorididae (*Gymnodoris*); and (4) Phyllidiidae (*Phyllidia*, *Phyllidiopsis*). Wide variation in sperm morphology in examined Dendronotoidea (Lomanotidae [*Lomanotus*], Hancockiidae [*Hancockia*], Tritoniidae [*Marianina*]) suggests the possibility that this is not a natural assemblage. Among the heteroproct Aeolidoidea, two groups can be discerned: (1) Aeolididae (*Aeolidiella*), Facelinidae (*Pteraeolidia*, *Favosinus*), Glaucidae (*Glaucus*, *Glaucilla*, *Austroelisis*); and (2) Flabellinidae (*Flabellina*, *Coryphella*). Representatives of the Apleioprocta await examination. At present, available sperm data for the Nudibranchia (or in fact most opisthobranch taxa) are insufficient to reach definitive conclusions concerning relationships with other opisthobranchs. A close relationship between the Anthobranchia and pleurobranchid notaspideans seems evident, though on the basis of comparative anatomy it seems likely that both groups have retained sperm features from a common ancestral stock.

INTRODUCTION

Nudibranchs comprise one of the most well known and visually conspicuous groups of marine gastropods (THOMPSON, 1976). Their striking color patterns and diverse morphology have made them favored subjects for aquatic photography, but in terms of taxonomic importance, these same factors have led to the creation of numerous very small or monotypic families or genera now recognized as superfluous (WILLAN, 1988). The order Nudibranchia contains perhaps as many as 1000 species (BOSS, 1982) and is usually divided into four superfamilies—Doridoidea, Aeolidoidea, Arminoidea and Dendronotoidea—distributed between the suborders Anthobranchia (Doridoidea) and Cladobranchia (containing the three other superfamilies) (WILLAN & COLEMAN, 1984). A number

of important systematic and phylogenetic problems remain to be settled in the study of the Nudibranchia such as the origin of the group and the relationships between constituent superfamilies and families.

Recent studies have established beyond question that spermatozoan fine structure is an extremely useful indicator of taxonomic affinity within the Mollusca (POPHAM, 1979; HODGSON *et al.*, 1988; HEALY, 1989a, b), particularly in the class Gastropoda (GIUSTI, 1971; GIUSTI & SELMI, 1982; KOHNERT & STORCH, 1984; KOIKE, 1985; HEALY, 1982-1988; HEALY & WILLAN, 1984; HODGSON & BERNARD, 1988). Among the Gastropoda, the subclass Prosobranchia has been studied extensively with regard to comparative sperm morphology and sperm development, partly because of the occurrence of sperm dimorphism in many taxa (for a full list of references see GIUSTI & SELMI, 1982; KOHNERT & STORCH, 1984; KOIKE, 1985; HEALY, 1988a). By comparison, few ultrastructural studies of opisthobranch spermatozoa have been carried out (Pyrami-

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delloidea HEALY, 1988b; the cephalaspidean *Tornatina* sp., HEALY, 1982a; Notaspidea, HEALY & WILLAN, 1984; Anaspidea, THOMPSON & BEBBINGTON, 1969, 1970; THOMPSON, 1973; KUBO & ISHIKAWA, 1981). In a pioneering paper, THOMPSON (1973) presented a broad outline of sperm ultrastructure within the Opisthobranchia (including some nudibranchs) and Pulmonata, though with primary emphasis on the helical form of the midpiece and nucleus, rather than morphology of the acrosomal complex. Earlier, THOMPSON (1966) provided the first reconstruction of a nudibranch spermatozoon using transmission electron microscopy (TEM) (allosperm of *Archidoris pseudoargus* Rapp). Recent studies of nudibranch spermiogenesis include those on *Spurilla neapolitana* (Delle Chiaje) (EYSTER & ECKELBARGER, 1979; ECKELBARGER & EYSTER, 1981; ECKELBARGER, 1982) and *Hypselodoris tricolor* (Cantaine) (MEDINA *et al.*, 1985, 1986, 1988a). SCKMEKEL (1971), HOLMAN (1972), and MEDINA *et al.* (1988b) also include ultrastructural observations on mature spermatozoa of nudibranchs: SCHMEKEL (1971) was in fact the first worker to demonstrate full details of the acrosome in any nudibranch (for *Doris verrucosa* Linné). In addition to these electron microscopical studies, ROGINSKAYA (1964, light microscopy) has reported dimorphic sperm nuclei in seven species of *Coryphella*, but only a single type of nucleus in spermatozoa of 22 other nudibranchs (representing the Doridoidea, Dendronotoidea, and Aeolidioidea).

The aims of the present study are firstly to document sperm morphology throughout the Nudibranchia, and secondly to determine whether or not sperm characters can be used to resolve taxonomic and/or phylogenetic problems within the group. In order to achieve these goals we have examined as wide a range of taxa as possible (38 species [27 at TEM level] from both suborders and all four superfamilies) and where available, incorporated TEM data from previously studied species.

We dedicate this paper to the memory of T. E. Thompson, a tireless worker devoted to the study of the Opisthobranchia (especially Nudibranchia) and a firm believer in the relevance of "new" fields of research such as sperm ultrastructure to the study of molluscan taxonomy and phylogeny.

MATERIALS AND METHODS

A total of 38 species were collected for this study from localities in Queensland (QLD), New South Wales (NSW), and Papua New Guinea (PNG) (Table 1). Of these species 27 were processed for TEM while the remaining 11 contained only sufficient spermatozoa to determine nuclear and whole sperm length using light microscopy. Voucher specimens of all species examined have been deposited at the Australian Museum (Sydney).

In most of the species processed for TEM, tissues from freshly gathered animals were fixed in 3% glutaraldehyde (prepared in 0.2 M phosphate buffer) at 0–4°C. Post-glutaraldehyde processing of PNG material could not be

carried out until return to Brisbane, resulting in a primary fixation period of three weeks. Although this delay did adversely affect the quality of fixation in some instances, spermatozoa were always adequately preserved for TEM.

Small (1–2 mm³) portions of the hermaphrodite duct, ampulla, and/or ovotestis were processed depending on the reproductive state of available animals (Table 1). After glutaraldehyde fixation, tissues were rinsed thoroughly in cold 0.2 M phosphate buffer, then placed in a 1% osmium tetroxide solution (prepared in 0.2 M phosphate buffer) for 80 min at 0–4°C. Following osmication, the tissues were rinsed in cold buffer, dehydrated in a graded ethanol series, and embedded in Spurr's epoxy resin.

Tissues from *Sclerodoris* cf. *apiculata*, *Dendrodoris nigra*, *Glaucilla marginata*, and *Glaucus atlanticus* were obtained from specimens fixed in seawater-formalin. After thorough rinsing in seawater, tissue samples of these four species followed the processing schedule outlined above.

Ultrathin sections were cut using an LKB IV Ultratome and collected on 200 mesh uncoated copper grids. Specimen-bearing grids were then stained with uranyl acetate and lead citrate according to the method of DADDOW (1983) and examined with an Hitachi 300 TEM operated at 75 kV. Whole spermatozoa were observed using an Olympus microscope adjusted for phase-contrast microscopy.

RESULTS

In view of the large number of nudibranch species examined during the course of this study, and in order to avoid much repetitious description, we have adopted a collative approach in the presentation of our results. The work is subdivided on the basis of the superfamily to which each taxon belongs—each section consisting of a detailed description for a representative species (*e.g.*, *Chromodoris annae* for Doridoidea), followed by notes summarizing sperm morphology in other members of the superfamily. As far as possible, descriptions for each taxon are supported by micrographs or line drawings. Where spermatozoa were absent or present only in low numbers within the hermaphrodite duct or ampulla our observations were limited to ovotesticular sperm (see Table 1). Aside from occasional variation in nuclear substructure and granule content of the glycogen helix, we found no morphological differences between sperm from the hermaphrodite duct, the ampulla, or the ovotestis in any given species. Table 2 provides a summary of measurements for sperm components in each species examined at the ultrastructural level.

DORIDOIDEA

CHROMODORIDIDAE—*Chromodoris annae* (Bergh) Acrosomal Complex

The acrosomal vesicle is spheroidal (0.13 μ m long, 0.12 μ m wide), membrane-bound, and rests in a shallow anterior depression of the acrosomal pedestal (Figure 1A, B). The pedestal is conical, 0.8–0.85 μ m long (including

Table 1
Species examined in this study using TEM.

Species	Locality	Fixation, tissue (for TEM)	Sperm length (μm)
DORIDOIDEA			
HEXABRANCHIDAE			
<i>Hexabranhus sanguineus</i> (Rüppell & Leuckart, 1828)	Shag Rock, QLD	Glut., hd/amp.	390
POLYCERIDAE			
<i>Tambja</i> cf. <i>oliva</i> Meyer, 1977	Madang lagoon, PNG	Glut., hd/amp.	135–150
<i>Kaloplocamus yatesi</i> (Angas, 1864)	Coffs Harbour, NSW	Glut., hd/amp.	270–280
GYMNODORIDIDAE			
<i>Gymnodoris</i> sp.	Madang lagoon, PNG	Glut, ovot.	425–440
CHROMODORIDIDAE			
<i>Chromodoris annae</i> Bergh, 1877	Madang lagoon, PNG	Glut., hd/amp.	270–280
<i>C. magnifica</i> (Quoy & Gaimard, 1832)	Madang lagoon, PNG	Glut., hd/amp.	270
<i>C. lochi</i> Rudman, 1982	Astralabe Bay, PNG	Glut., hd/amp.	n.d.
<i>Glossodoris atromarginata</i> (Cuvier, 1804)	Shag Rock, QLD	Glut., ovot.	n.d.
<i>Miamira magnifica</i> Eliot, 1910	Coffs Harbour, NSW	—	100–125
<i>Ceratosoma tenue</i> Abraham, 1876	Coffs Harbour, NSW	—	200–215
<i>Hypselodoris</i> cf. <i>nigrostriata</i> (Eliot, 1904)	Coffs Harbour, NSW	—	465–475
DORIDIDAE			
<i>Rostanga arbutus</i> (Angas, 1864)	Hastings Point, NSW	Glut, ovot.	245–250
<i>Jorunna pantherina</i> (Angas, 1864)	Hastings Point, NSW	Glut., hd/amp.	190
<i>Doriopsis granulosa</i> Pease, 1860	Coffs Harbour, NSW	Glut., hd/amp.	215
<i>Sclerodoris</i> cf. <i>apiculata</i> (Alder & Hancock, 1864)	Macleay, NSW	SWF, ovot.	240–245
<i>Asteronotus cespitosus</i> (Hasselt, 1824)	north of Madang, PNG	Glut., hd/amp.	310–315
<i>Halgerda tessellata</i> (Bergh, 1880)	Madang lagoon, PNG	—	340–350
<i>Discodoris concinna</i> (Alder & Hancock, 1864)	Coffs Harbour, NSW	—	470–475
DENDRODORIDAE			
<i>Dendrodoris nigra</i> (Stimpson, 1855)	south of Port Macquarie, NSW	NSW SWF, hd/amp.	380–400
<i>Doriopsis miniata</i> (Alder & Hancock, 1864)	Hastings Point, NSW	—	587–612
PHYLLIDIIDAE			
<i>Phyllidia ocellata</i> Cuvier, 1804	Coffs Harbour, NSW	—	312–340
<i>Phyllidia nobilis</i> Bergh, 1869	Shag Rock, QLD	Glut., hd/amp.	310–340
<i>Phyllidiopsis cardinalis</i> Bergh, 1876	Astralabe Bay, PNG	Glut., hd/amp.	165–175
<i>Phyllidiopsis striata</i> Bergh, 1888	Madang lagoon, PNG	—	215–240
AEOLIDOIDEA			
FACELINIDAE			
<i>Pteraeolidia ianthina</i> (Angas, 1864)	Tangalooma Channel, QLD	Glut., hd/amp.	390–395
<i>Favorinus japonicus</i> Baba, 1949	Hastings Point, NSW	Glut., ovot.	n.d.
GLAUCIDAE			
<i>Glaucus atlanticus</i> Forster, 1777	Fingal Beach, NSW	SWF, hd/amp.	160–170
<i>Glaucilla marginata</i> Bergh, 1860	Fingal Beach, NSW	SWF, hd/amp.	n.d.
<i>Austraeolis ornata</i> (Angas, 1864)	Hastings Point, NSW	—	340–345
AEOLIDIIDAE			
<i>Aeolidiella indica</i> Bergh, 1888	Coffs Harbour, NSW	Glut, hd/amp.	200–225
<i>Aeolidiella alba</i> Risbec, 1928	Hastings Point, NSW	—	187–200
FLABELLINIDAE			
<i>Flabellina rubrolineata</i> (O'Donoghue, 1929)	Coffs Harbour, NSW	Glut., hd/amp.	260–270
DENDRONOTOIDEA			
LOMANOTIDAE			
<i>Lomanotus vermiformis</i> Eliot, 1908	Stradbroke Is., QLD	Glut., hd/amp.	200–230

Table 1
Continued

Species	Locality	Fixation, tissue (for TEM)	Sperm length (μm)
HANCOCKIIDAE			
<i>Hancockia</i> sp.	Madang lagoon, PNG	Glut., ovot.	n.d.
TRITONIIDAE			
<i>Marianina rosea</i> (Provot-Fol, 1930)	north of Madang, PNG	Glut., ovot.	n.d.
<i>Marionia cyanobanchiata</i> (Rüppell & Leuckart, 1831)	Coffs Harbour, NSW	—	320–330
ARMINOIDEA			
ARMINIDAE			
<i>Dermatobranchus fortunata</i> Bergh, 1874	Madang lagoon, PNG	Glut, ovot.	n.d.
DORIDOMORPHIDAE			
<i>Doridomorpha gardineri</i> Eliot, 1906	Madang lagoon, PNG	Glut., hd/amp.	n.d.

Abbreviations: NSW, New South Wales; PNG, Papua New Guinea; QLD, Queensland; Glut., glutaraldehyde; SWF, seawater formalin; hd/amp., hermaphrodite duct and/or ampulla; ovot., ovotestis; n.d., not determined.

a short [0.23 μm] overlap zone with the nuclear apex), and lacks any enveloping membrane (Figure 1A–D). Longitudinal sections through the pedestal often reveal fine parallel striations, arranged at approximately 20° relative to the transverse plane and repeating at a distance of 12.5 nm (Figure 1D).

Nucleus

The nucleus is 7–7.5 μm long, helically coiled, and circular in transverse section (Figure 1E, F). Contents of the nucleus are finely granular and evenly electron dense. Basally, a shallow (0.4–0.45 μm deep) invagination is filled by a bell-shaped centriolar derivative continuous with the axoneme/coarse-fiber complex (Figure 1E, F). Both within and beyond the nuclear invagination the microtubular nature of the axonemal doublets and singlets is obscured by dense material (Figure 1E, G). The doublets always remain distinct from the coarse fibers, though usually in contact with them (Figure 1E). Slight overlap occurs between the base of the nucleus and the thin, anterior extremity of the mitochondrial derivative (Figure 1E, F). A subnuclear ring occurs in this region of the spermatozoon (Figure 1F).

Midpiece

The midpiece in *Chromodoris annae* is composed of the axoneme/coarse-fiber complex ensheathed by the mitochondrial derivative (Figure 1F–L) and measures approximately 260 μm . Immediately posterior to the nucleus, the coarse fibers that surround the 9+2 axoneme are thick (0.1–0.12 μm wide) and prominently banded (periodicity 45 nm) and are surrounded by dense glycogen deposits and a thin anterior extension of the mitochondrial deriv-

ative (Figure 1E, F). As these fibers progress further into the midpiece, they rapidly decrease in diameter, and their periodic substructure becomes less evident (Figure 1F, G). The mitochondrial derivative consists of paracrystalline and matrix materials which enclose: (1) the glycogen (or primary) helix—a helical compartment containing glycogen granules—and (2) the axoneme/coarse-fiber complex (Figure 1F–L). Oblique longitudinal and transverse sections through the midpiece best show the helical, lattice-like substructure of the paracrystalline material (Figure 1H, I). The matrix component of the mitochondrial derivative is subdivided into helical tracts, two of which are expanded to form secondary helices in the immediate post-nuclear region of the midpiece (Figure 1F, H–J). Progressing posteriorly, first one (Figure 1G) then both (Figure 1K) of these secondary helices are lost. Similarly, the glycogen helix diminishes in size along the length of the midpiece and is absent from the posterior region (Figure 1L). The terminal region of the midpiece consists of the axoneme enclosed by the cylindrical extension of the mitochondrial derivative (Figure 1L).

Glycogen Piece

A glycogen piece, in the strict sense, is absent in *Chromodoris annae*. Instead, a cap-shaped body (length 0.13 μm), probably a modified annulus, seals off the degenerating axoneme to form the distal end of the spermatozoon (Figure 1L).

Other CHROMODORIDIDAE [TEM: *Chromodoris magnifica* (Quoy & Gaimard), *Chromodoris lochi* Rudman, *Glossodoris atromarginata* (Cuvier)—(not illustrated);

Table 2
Comparative sperm ultrastructure in species studied.

Species	Acrosomal complex		Nucleus	Centriolar derivative	Fiber periodicity	Midpiece	Glycogen piece	Annulus
	Vesicle	Pedestal						
DORIDOIDEA								
HEXABRANCHIDAE								
<i>Hexabranchnus sanguineus</i>	large (0.25 μm)	short (0.17 μm)	short (4 μm)	bell shaped	nd.	w/g.h. only	?absent	?present
POLYCERIDAE								
<i>Tambija</i> cf. <i>oliva</i>	large (0.18 μm)	short (0.3 μm)	short (4 μm)	bell shaped	n.d.	w/g.h. only	absent	cap shaped
<i>Kaloplocamus yatesi</i>	medium (0.13 μm)	long (1.4 μm), coarse bands	short (4 μm)	bell shaped	44 nm	w/g.h. only	present	ring shaped
GYMNODORIDIDAE								
<i>Gymnodoris</i> sp.	medium (0.15 μm)	long (2.1 μm), coarse bands	short (4 μm)	bell shaped	37 nm	w/g.h. only	?absent	?present
CHROMODORIDIDAE								
<i>Chromodoris annae</i>	medium (0.13 μm)	long (0.8 μm), fine bands	short (7.5 μm)	bell shaped	45 nm	g.h. & 2° keels	absent	cap shaped
DORIDIDAE								
<i>Rostanga arbutus</i>	medium (0.14 μm)	long (0.6 μm), fine bands	short (4 μm)	bell shaped	45 nm	w/g.h. only	present	ring shaped
<i>Jorunna pantherina</i>	medium (0.13 μm)	long (0.6 μm), electron lucent bands	short (8 μm)	bell shaped	45 nm	w/g.h. only	present	ring shaped
<i>Doriopsis granulosa</i>	medium (0.15 μm)	long (0.56 μm)	long (14 μm)	bell shaped	52 nm	w/g.h. only	present	ring shaped
<i>Sclerodoris</i> cf. <i>apiculata</i>	large (0.2 μm)	short (0.2–0.3 μm)	short (4 μm)	bell shaped	54 nm	w/g.h. only	?absent	?present
<i>Asteronotus cespitosus</i>	large (0.2 μm)	short (0.2–0.3 μm)	short (4 μm)	bell shaped	n.d.	w/g.h. only	?absent	?present
DENDRODORIDAE								
<i>Dendrodoris nigra</i>	medium (0.13 μm)	long (0.8 μm)	short (7 μm)	bell shaped	n.d.	w/g.h. only	?absent	?present
PHYLLIDIIDAE								
<i>Phyllidia nobilis</i>	oblong (0.18 μm)	long (0.9–1.0 μm)	long (12–15 μm)	bell shaped	54 nm	w/g.h. only	?present	?present
<i>Phyllidiopsis cardinalis</i>	oblong (0.18 μm)	long (0.9–1.0 μm)	long (15 μm)	bell shaped	54 nm	w/g.h. only	?present	?present
AEOLIDOIDEA								
FACELINIDAE								
<i>Pteraeolidia ianthina</i>	small (0.09 μm)	long (2.3 μm), entwined w/nucleus	short (4.4 μm) w/keels	solid, conical	55 nm	g.h. & 2° keels	?absent	?present
<i>Favorinus japonicus</i>	small (0.07 μm)	long(?), entwined w/nucleus	short (5 μm) w/keel	n.d.	n.d.	g.h. & 2° keels	?absent	?present

Table 2
Continued

Species	Acrosomal complex		Nucleus	Centriolar derivative	Fiber periodicity	Midpiece	Glycogen piece	Annulus
	Vesicle	Pedestal						
GLAUCIDAE								
<i>Glaucilla marginata</i>	small (0.08 μm)	long (2 μm), entwined w/nucleus	short (5 μm) w/keels	solid, conical	n.d.	g.h. & 2° keels	?absent	?present
AEOLIDIIDAE								
<i>Aeolidiella indica</i>	n.d.	long(?), entwined w/nucleus	short (5 μm) w/keels	solid, conical	n.d.	g.h. & 2° keels	?absent	?present
FLABELLINIDAE								
<i>Flabellina rubrolineata</i>	small (0.09 μm)	long (1.8–2.0 μm) in nucl. groove	short (7 μm) w/keel	solid, conical	40 nm	w/g.h. only	present	ring shaped
DENDRONOTOIDEA								
LOMANOTIDAE								
<i>Lomanotus vermiciformis</i>	oblong (0.56 μm)	short (0.2–0.25 μm)	short (4 μm)	bell shaped	48 nm	w/g.h. only	present	?ring shaped
HANCOCKIIDAE								
<i>Hancockia</i> sp.	large (0.22 μm)	short (0.2–0.25 μm)	short(?)	bell shaped	54 nm	w/g.h. only	?absent	?present
TRITONIIDAE (MARIANININAE)								
<i>Marianina rosea</i>	small (0.09 μm)	short (0.1 μm)	short(?) w/keels	bell shaped	52 nm	w/g.h. only	?absent	?present
ARMINOIDEA								
DERMATOBRANCHIDAE								
<i>Dermatobranchius fortunata</i>	n.d.	short (?)	short(?) w/keels	n.d.	n.d.	w/g.h. only	?absent	?present
DORIDOMORPHIDAE								
<i>Doridomorpha gardineri</i>	small (0.08 μm)	medium (0.4 μm)	short(?)	bell shaped	52 nm	g.h. & 2° keel	present	ring shaped

Abbreviations: g.h., glycogen helix; n.d., not determined

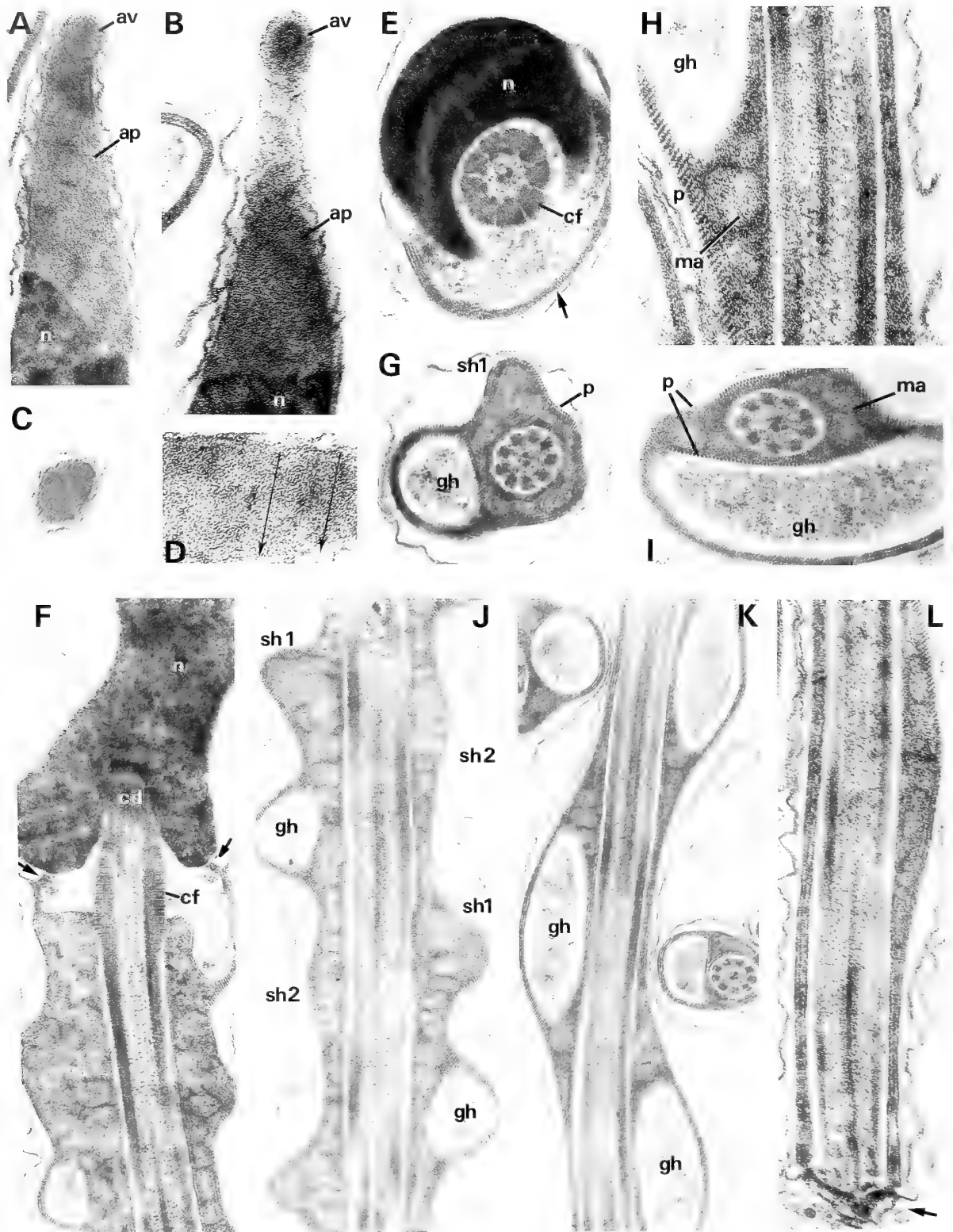
Figure 1A-L: *Chromodoris annae*.

Figure 1A, B. Longitudinal sections (LS) through acrosomal complex and nuclear apex (1A $\times 57,600$; 1B $\times 63,000$).

Figure 1C. Transverse section (TS) acrosomal pedestal ($\times 72,000$).

Light microscopy: *Miamira magnifica* Eliot; *Ceratosoma tenue* Abraham; *Hypselodoris* cf. *nigrostriata* (Eliot)]

Spermatozoal features of other *Chromodoris* species are essentially as outlined above for *C. annae*. *Glossodoris atromarginata* differs from *Chromodoris* spp. in having a prominent helical keel present in the nucleus. Although no data on the acrosome in *Glossodoris atromarginata* could be obtained, the distal region of the spermatozoon appears to be cap-shaped and composed of nine segments. Sperm length is extremely variable in the Chromodorididae. The shortest was observed in *Miamira magnifica* (100–125 μm) and the longest, those of *Hypselodoris* cf. *nigrostriata* (465–475 μm) (see Table 1).

DORIDIDAE [TEM: *Rostanga arbutus* (Angas) (Figure 2A–G), *Jorunna pantherina* (Angas) (Figure 2H–M), *Doriopsis granulosa* Pease (Figure 3E–I), *Sclerodoris* cf. *apiculata* (Alder & Hancock) (Figure 3A–D), *Asteronotus cespitosus* (Hasselt) (see Figure 11); Light microscopy: *Halgerda tessellata* (Bergh), *Discodoris concinna* (Alder & Hancock), *Hypselodoris* cf. *nigrostriata* (Eliot, 1904)]

The Dorididae show marked variation in the morphology of the nucleus and acrosomal complex. *Rostanga arbutus* (Figure 2A–G), *Jorunna pantherina* (Figure 2H–M) and *Doriopsis granulosa* (Figure 3E–I) show similar acrosomal and midpiece features to those described for *Chromodoris annae*; *Rostanga arbutus* in fact also exhibits fine striations within the pedestal (Figure 2B). Nuclei of *Doriopsis granulosa* (12–14 μm) are appreciably longer than those of other dorids (4–8 μm), but helically shaped like *Jorunna pantherina* (Figure 2I), *Chromodoris* spp., and *Sclerodoris* cf. *apiculata* (Figure 3A). Unlike *Chromodoris annae*, a glycogen piece is present in spermatozoa of *Rostan-*

ga arbutus (length 0.4 μm , Figure 2E, G), *Jorunna pantherina* (length 1.25 μm , Figure 2M) and *Doriopsis granulosa* (length 0.58 μm , Figure 3I). The axoneme persists to the terminal edge of the glycogen piece in *Doriopsis granulosa* (Figure 3I). Axonemal microtubules are absent from the glycogen piece and the distal portion of the midpiece of *Jorunna pantherina* (Figure 2M). Similarly, the glycogen piece of *Rostanga arbutus* also contains only dense granules (Figure 2E, G), though some transverse sections reveal that the axoneme is present in the distal region of the midpiece. A subnuclear ring is observed in all studied members of the Dorididae (e.g., Figures 2J, 3C, F).

Sperm length is variable in the Dorididae, ranging from 190 μm in *Jorunna pantherina* to 475 μm in *Discodoris concinna* (see Table 1).

Spermatozoa of *Sclerodoris* cf. *apiculata* (Figure 3A–D) and *Asteronotus cespitosus* (see Figure 11) differ from other investigated dorids and the Chromodorididae principally in having a larger acrosomal vesicle (length 0.18 μm , breadth 0.2–0.24 μm) positioned on a short (0.2–0.3 μm) pedestal (Figure 3B). The fibrous, inflated appearance of the nucleus in *Asteronotus cespitosus* is possibly due to osmotic stress, though in other nudibranch species where this phenomenon was observed (e.g., *Hexabranchus sanguineus* [Figure 3J, K], *Kaloplocamus yatesi* [Figure 4E], *Lomanotus vermiformis* [Figure 9C]) other sperm organelles show little sign of osmotic stress. The shallow basal invagination of the nucleus in *Sclerodoris* cf. *apiculata* is occupied by a bell-shaped centriolar derivative and the distal accessory sheath (Figure 3C). Coarse fibers of *Sclerodoris* have a banding periodicity of 54 nm. Morphology of the midpiece in *Sclerodoris* cf. *apiculata* and *Asteronotus cespitosus* appears similar to other dorids (Figure 3C, D), though in *Sclerodoris* cf. *apiculata*, the matrix component of the mitochondrial derivative is lamellate anteriorly (Figure 3C). Unfortunately

Figure 1D. Striated substructure of pedestal. Pedestal lying horizontally (long arrows indicating direction of striations) ($\times 84,000$).

Figure 1E. TS junction of nucleus and midpiece. Note coarse fibers (surrounding 9+2 axoneme), and glycogen from neck region of midpiece. Arrow indicates anterior extremity of mitochondrial derivative ($\times 44,600$).

Figure 1F. LS nucleus-midpiece junction. Arrows indicate subnuclear ring ($\times 30,000$).

Figure 1G. TS proximal region of midpiece showing glycogen helix and secondary helix ($\times 42,000$).

Figure 1H. LS detail of midpiece showing paracrystalline and matrix materials ($\times 75,600$).

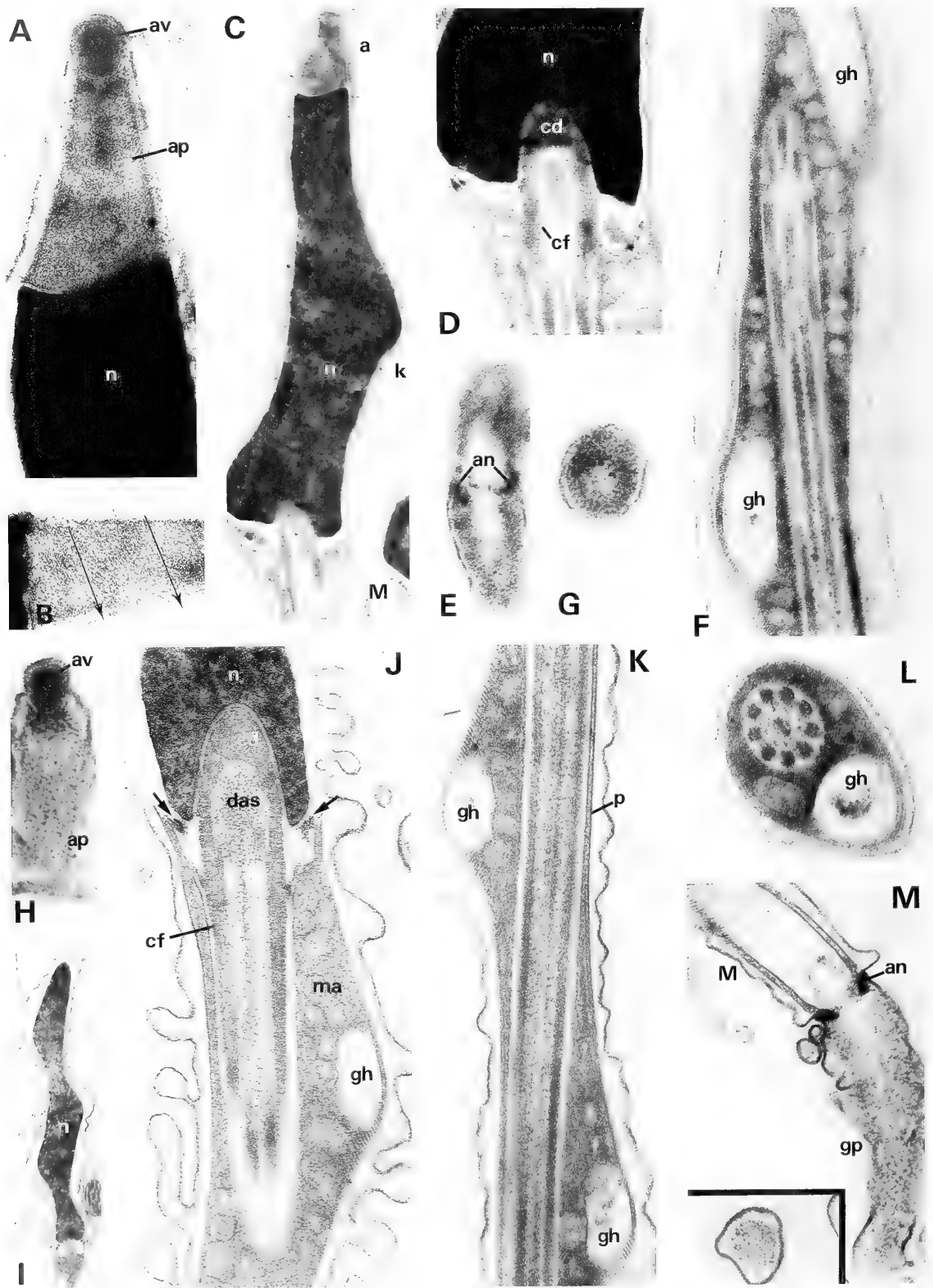
Figure 1I. Oblique TS of midpiece. Matrix and paracrystalline components of mitochondrial derivative visible ($\times 44,500$).

Figure 1J. LS proximal region of midpiece with two secondary helices ($\times 30,000$).

Figure 1K. LS middle region of midpiece. Note absence of secondary helices ($\times 30,000$).

Figure 1L. LS through terminal region of spermatozoon. Cap-shaped structure (arrow) probably represents a form of annulus ($\times 50,000$).

Abbreviations: ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; gh, glycogen helix; ma, matrix material; n, nucleus; p, paracrystalline material; sh1, sh2, secondary helices.



the terminal region of the spermatozoon was not observed for *Sclerodoris* cf. *apiculata* or *Asteronotus cespitosus*, despite many hours of TEM observation. Possibly the glycogen piece is reduced to a vestigial cap as noted above for the chromodorids (see Figure 1L).

HEXABRANCHIDAE [TEM: *Hexabranchnus sanguineus* (Rüppell & Leuckart) (Figure 3J, K)]

Sperm features of *Hexabranchnus sanguineus*, in particular the structure of the acrosomal complex (Figure 3J, K), are very similar to those observed in the dorids *Sclerodoris* cf. *apiculata* and *Asteronotus cespitosus*. Sperm nuclei of *Hexabranchnus sanguineus* (Figure 3K) are round and coarsely fibrous as observed in *Asteronotus cespitosus*. A bell-shaped centriolar derivative fills the shallow basal invagination of the nucleus (Figure 3K). The immediate post-nuclear region of the midpiece shows lamellar organization of the matrix component of the mitochondrial derivative. No data on the presence or morphology of the glycogen piece could be obtained. Mature spermatozoa measure approximately 390 μm .

POLYCERIDAE [TEM: *Tambja* cf. *oliva* Meyer, *Kaloplocamus yatesi* (Angas)]

The two investigated polycerids differ markedly from each other in acrosomal and glycogen piece morphology.

In *Tambja* cf. *oliva* (not illustrated), the acrosomal complex is similar to those of *Sclerodoris* cf. *apiculata*, *Asteronotus cespitosus*, and *Hexabranchnus sanguineus*. The nucleus is short (4 μm), fibrous, and rounded in appearance with a shallow basal invagination (0.3 μm deep) occupied by a bell-shaped centriolar derivative. Midpiece morphology resembles that observed in most other dorids (one glycogen helix, no secondary helices), and the glycogen piece is reduced to a dense cap-shaped structure similar to *Chromodoris annae* (see Figure 1L). A subnuclear ring is present.

Spermatozoa of *Kaloplocamus yatesi* also possess a short (3–4 μm), fibrous nucleus with a shallow (0.33 μm deep) basal invagination to accommodate the centriolar derivative and anterior portion of the distal accessory sheath (Figure 4E). The coarse fibers, which do not enter the nuclear invagination, have a maximum thickness of 0.08 μm and exhibit primary periodic banding of 44 nm. The acrosomal pedestal (length 1.44 μm) is significantly longer than those of other doridoids (range 0.2–0.85 μm), and shows coarse transverse banding (composed of alternating dense and electron-lucent bands; distance between centers of dense bands, 75 nm) (Figure 4C). However, the shape of the pedestal (conical, angularly overlapping the nuclear apex, Figure 4C), size of the acrosomal vesicle (length 0.13 μm , breadth 0.12 μm , Figure 4C) and morphology of the midpiece (Figure 4C–F) are essentially as observed in

Figure 2A–L: Figure A–F, *Rostanga arbutus*;
Figure G–L, *Jorunna pantherina*

Figure 2A. LS acrosomal complex and nuclear apex ($\times 56,000$).

Figure 2B. Striated substructure of pedestal (striation direction indicated by long arrows). Pedestal lying horizontally ($\times 58,000$).

Figure 2C. LS acrosomal complex, nucleus (showing helical keel) and proximal portion of midpiece ($\times 18,500$).

Figure 2D. LS junction of nucleus and neck region of midpiece ($\times 35,000$).

Figure 2E. Annulus at junction of midpiece and glycogen piece ($\times 32,000$).

Figure 2F. LS midpiece ($\times 32,000$).

Figure 2G. TS glycogen piece. The lumen contains no axoneme ($\times 38,000$).

Figure 2H. LS acrosomal complex showing angled striations in the pedestal ($\times 56,000$).

Figure 2I. LS nucleus showing helical coiling ($\times 9,300$).

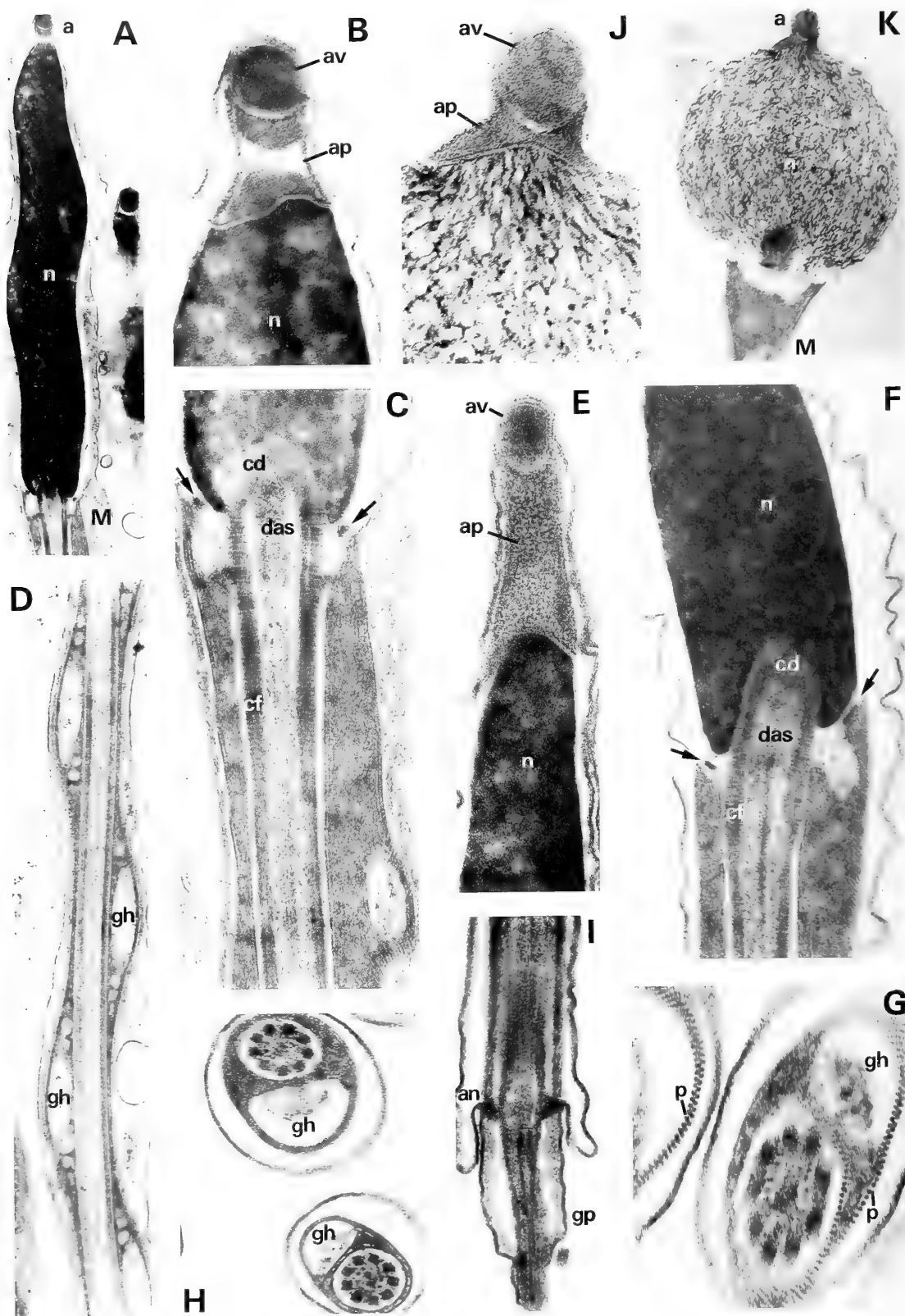
Figure 2J. LS junction of nucleus and proximal region of midpiece. Arrows indicate subnuclear ring ($\times 47,000$).

Figure 2K. LS midpiece ($\times 42,000$).

Figure 2L. TS midpiece ($\times 47,000$).

Figure 2M. LS junction of midpiece and glycogen piece ($\times 38,000$). Inset: TS terminal region of glycogen piece ($\times 50,000$).

Abbreviations: a, acrosomal complex; an, annulus; ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; k, nuclear keel; M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material.



chromodorids and other dorids. A subnuclear ring is present (Figure 4E). The axoneme persists within the distal region of the midpiece but degenerates into a rod-shaped structure within the lumen of the glycogen piece (Figure 4G). The glycogen piece measures 0.6 μm in length and is preceded by an annulus attached to the plasma membrane (Figure 4F, G). Mature spermatozoa of *Tambja* cf. *oliva* measure 135–150 μm , while those of *Kaloplocamus yatesi* measure 270–280 μm .

GYMNODORIDIDAE [TEM: *Gymnodoris* sp.]

Results obtained for *Gymnodoris* sp. closely match those described above for *Kaloplocamus yatesi* with the exception that the coarsely banded pedestal is longer in *Gymnodoris* sp. (2.1 μm), shows evidence of longitudinally aligned fibers, and features a prominent, unbanded lateral region (Figure 4B). The acrosomal vesicle measures 0.15 μm in length and 0.116 μm in breadth (Figure 4B). Figure 4C indicates the presence of an unbanded region of the pedestal in *Kaloplocamus yatesi* though in comparison with *Gymnodoris* sp. this feature is poorly developed. Nuclei of testicular spermatozoa are short (3–3.5 μm long) and uniformly electron dense (in contrast to the inflated, fibrous nuclei of *Kaloplocamus yatesi*) and lacking any keel(s). The morphology of the glycogen piece and distal region of the midpiece was not determined. Features of the midpiece of *Gymnodoris* sp. are as previously noted for *Kaloplocamus yatesi*, Chromodorididae, and Dorididae. Spermatozoa of *Gymnodoris* sp. are 425–440 μm long.

DENDRODORIDAE [TEM: *Dendrodoris nigra* (Stimpson) (not illustrated); Light microscopy: *Doriopsis miniata* (Alder & Hancock)]

Our limited TEM observations on mature spermatozoa of *Dendrodoris nigra* indicate similar sperm morphology to chromodorids and certain doridids, notably *Doriopsis granulosa*. The glycogen piece was not observed. Spermatozoa of *Doriopsis miniata* are notable in being the longest recorded for the Nudibranchia (587–612 μm), while those of *Dendrodoris nigra* measure 380–400 μm .

PHYLLIDIIDAE [TEM: *Phyllidia nobilis* Bergh, *Phyllidiopsis cardinalis* Bergh; Light microscopy: *Phyllidia ocellata* Cuvier, *Phyllidiopsis striata* Bergh]

In phyllidiid species examined with TEM, the acrosomal pedestal is slender, 0.9–1.0 μm long, and apically supports an oblong acrosomal vesicle (length 0.18 μm , breadth 0.08 μm) (Figure 5A, E). Often the pedestal is curved, occasionally to an exaggerated degree (Figure 5C) demonstrating the flexibility of this sperm component. As in many other doridoids, the bases of the acrosomal pedestal and nuclear apex are angularly overlapped in longitudinal sections (Figure 5A, C, E). Nuclei are long (12–15 μm in *Phyllidia* spp., 15–25 μm in *Phyllidiopsis* spp.), finely tapered anteriorly, and circular in transverse section. Although nuclei of *Phyllidiopsis* spp. show evidence of slight helical coiling (Figure 5B) nuclear keels appear to be absent in the Phyllidiidae. Basally, the nucleus exhibits a shallow invagination occupied largely by a bell-shaped

Figure 3A–K: Figure A–D, *Sclerodoris* cf. *apiculata*; Figure E–I, *Doriopsis granulosa*; Figure J, K, *Hexabranchnus sanguineus*

Figure 3A. LS acrosomal complex, nucleus, and proximal portion of midpiece ($\times 14,400$).

Figure 3B. LS detail of acrosomal complex and nuclear apex ($\times 60,000$).

Figure 3C. LS junction of nucleus and midpiece. Arrows indicate subnuclear ring ($\times 45,000$).

Figure 3D. LS midpiece ($\times 22,500$).

Figure 3E. LS acrosomal complex and nuclear apex ($\times 60,000$).

Figure 3F. LS junction of nucleus and midpiece. Subnuclear ring indicated by arrows ($\times 43,500$).

Figure 3G. Oblique TS midpiece showing paracrystalline layers ($\times 67,500$).

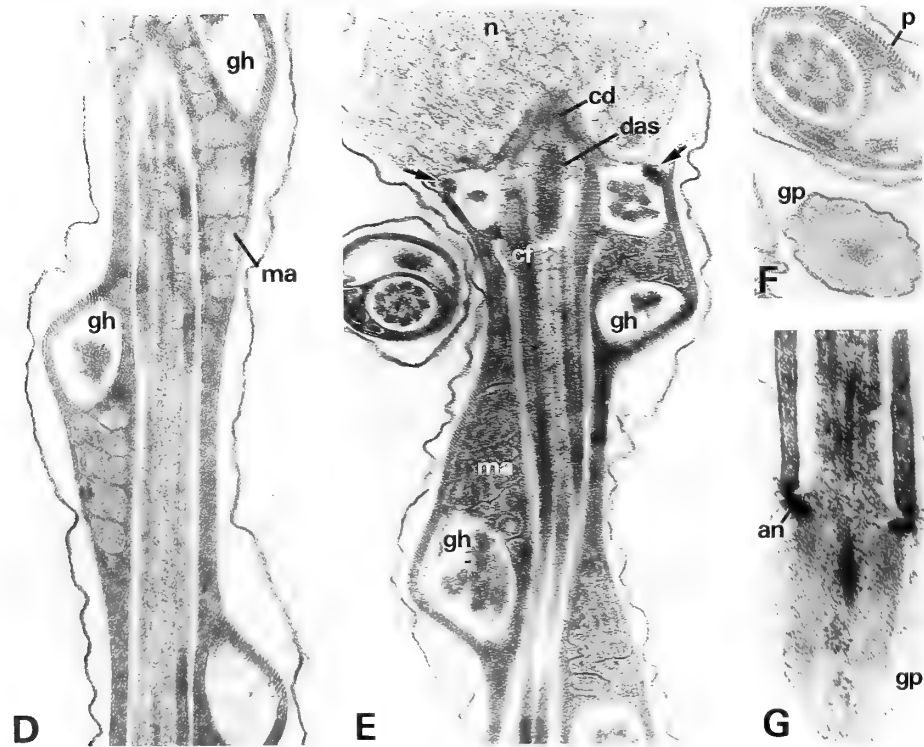
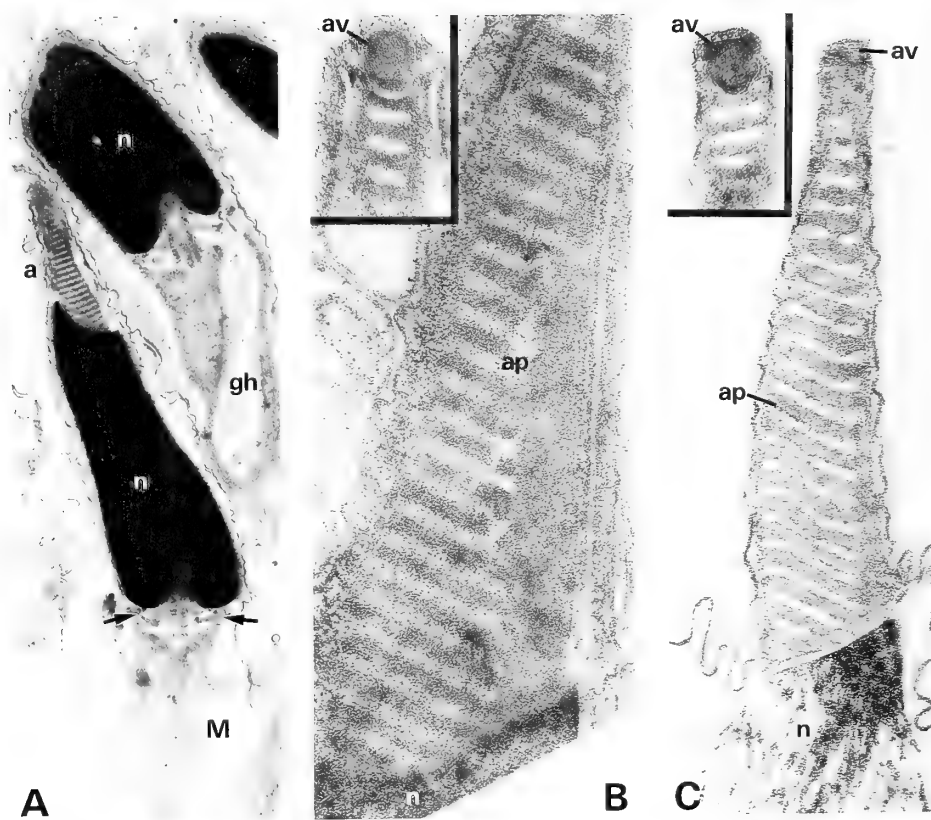
Figure 3H. TS showing reduction in size of midpiece from anterior (upper) to posterior (lower) regions ($\times 42,000$).

Figure 3I. LS junction of midpiece and glycogen piece showing annulus ($\times 45,000$).

Figure 3J. LS acrosomal complex and nuclear apex ($\times 60,000$).

Figure 3K. LS acrosomal complex, nucleus (fibrous, inflated), and proximal portion of midpiece ($\times 18,750$).

Abbreviations: a, acrosomal complex; an, annulus; ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material.



centriolar derivative continuous with the axoneme/coarse-fiber complex and penetrated by the central pair of axonemal microtubules (Figure 5F). Also present is a diffuse distal accessory sheath (partly extending into the nuclear invagination) and a subnuclear ring (Figure 5F). Immediately posterior to the nucleus, the glycogen helix is poorly developed and usually filled with membranes (Figure 5G, H). In this region of the midpiece, the matrix component of the mitochondrial derivative is lamellar in appearance (Figure 5G, H). Further posteriorly the glycogen helix becomes prominent (and partly filled with granular deposits, Figure 5D, I, J), but is absent in the most distal region of the midpiece (Figure 5K). Organization of matrix and paracrystalline components of the mitochondrial derivative is as described for other Doridoidea. Unfortunately the midpiece-glycogen junction was not observed in longitudinal section. Occasionally, transverse sections were obtained showing the 9+2 axoneme surrounded by nine granular blocks, each associated with an adjoining axonemal doublet (Figure 5L). It seems possible that these are transverse sections through a cap-shaped structure (? modified annulus) similar to those noted previously for *Chromodoris annae* (Figure 1L) and *Tambja* cf. *oliva*. Spermatozoa of phyllidiids range in length from 165–175 μm (*Phyllidiopsis cardinalis*) to 310–340 μm (*Phyllidia nobilis*) (Table 1).

AEOLIDOIDEA

FACELINIDAE [*Pteraeolidia ianthina* (Angas)]

Acrosome

The apical vesicle is small (0.09 μm long, 0.06 μm wide) and lies at the anterior extremity of the acrosomal pedestal (Figure 6B Inset). The pedestal of *Pteraeolidia ianthina*

(total length 2.3 μm) is extensively intertwined with the nuclear keels (Figure 6A–H).

Nucleus

The nucleus is short (4.4 μm), with a maximum of three or four helical keels posteriorly (decreasing to a single keel near the nuclear apex). The overlap between the acrosomal pedestal and the nucleus has already been described. Transverse and longitudinal sections through the base of the nucleus show that the coarse fibers are closely applied to the axonemal doublets (Figure 6I–M). Within and immediately outside the nuclear invagination, each doublet is connected to its adjoining doublets (Figures 6M, 7A). A solid, conical centriolar derivative occupies the innermost recess of the basal invagination of the nucleus (Figure 6I, J). To this structure are attached the coarse fibers (periodicity 55 nm) and the central pair of axonemal microtubules, the latter seemingly lacking any lumen (Figure 6I–M). A diffuse, distal accessory sheath surrounds the central pair of axonemal microtubules, both within the basal invagination of the nucleus (Figure 6K–M) and in the neck region of the midpiece (Figures 6L–M, 7A, B).

Midpiece

The neck region is characterized by deposits of membranous material (Figure 7A), pockets of unorganized dense granules (Figure 7B), and the axoneme/coarse-fiber complex, surrounded by outlying layers of paracrystalline material. A subnuclear ring is usually visible. Further posteriorly (Figure 7C–G) the following changes in midpiece structure occur: (1) the dense granules are organized into a single helix (glycogen helix); (2) the matrix material is helically subdivided; and (3) paracrystalline material forms the inner (periaxonemal) and outer walls of the mito-

Figure 4A–G: Figure A, B, *Gymnodoris* sp.;
Figure C–G, *Kaloplocamus yatesi*

Figure 4A. LS acrosomal complex, nucleus, and proximal region of midpiece. Arrows indicate subnuclear ring ($\times 13,300$).

Figure 4B. LS acrosomal complex. Note banded and unbanded portions of acrosomal pedestal. Inset: acrosomal vesicle ($\times 56,000$).

Figure 4C. LS acrosomal complex (with vesicle shown inset). Coarse banding of pedestal clearly visible ($\times 56,000$).

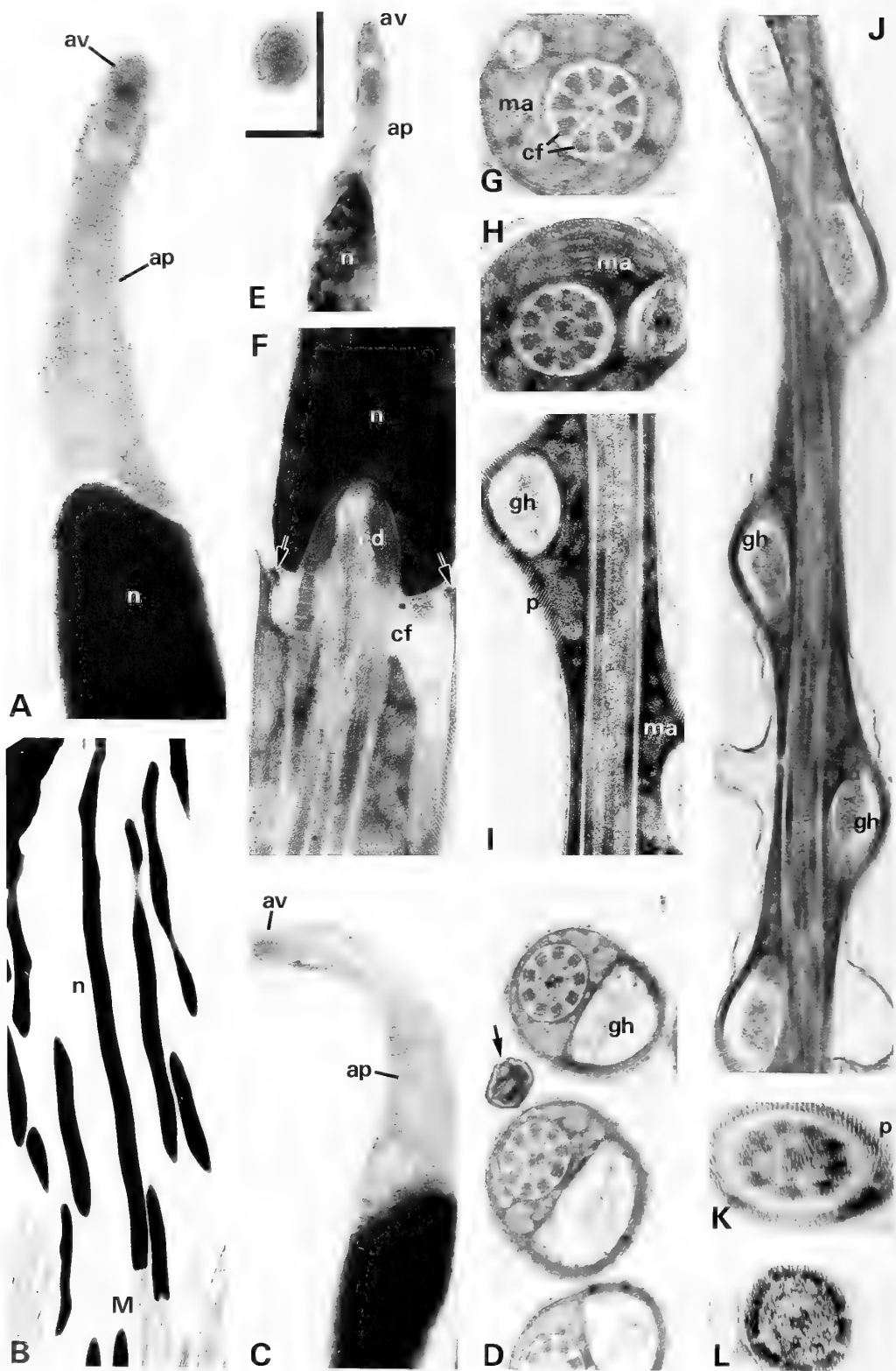
Figure 4D. LS anterior region of midpiece showing glycogen helix and subdivided matrix material ($\times 32,000$).

Figure 4E. LS junction of nucleus (fibrous) and midpiece. Arrows indicate subnuclear ring ($\times 32,000$).

Figure 4F. TS midpiece and glycogen piece ($\times 45,500$).

Figure 4G. LS junction of midpiece and glycogen piece. Note annulus ($\times 50,000$).

Abbreviations: a, acrosomal complex; an, annulus; ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material.



chondrial derivative, enclosing matrix, glycogen helix, axoneme, and coarse fibers. Aside from the glycogen helix, a secondary helix, formed only of the matrix and paracrystalline materials, occurs in the midpiece (Figure 7C–F). Towards the posterior region of the midpiece, the secondary helix is lost and the glycogen helix becomes greatly reduced in size (Figure 7E). Figure 7 (H, I) shows that the glycogen helix also ultimately disappears and that the axoneme is replaced by a deposit of fine granular material and packed membranes. In what is presumed to be close to the terminal region of the spermatozoon, the lumen of the midpiece is unoccupied. Although the midpiece is usually enclosed by the mitochondrial and plasma membranes (Figure 7F, G), spermatozoa lacking these membranes were also observed (Figure 7B, D top). No evidence of a glycogen piece or annulus could be found even after many hours of observation. Nevertheless in the absence of longitudinal sections through the terminal region of spermatozoa, we cannot unequivocally state that a glycogen piece or annulus is absent in *Pteraeolidia ianthina*. Total sperm length in *Pteraeolidia ianthina* is 390–395 μm .

GLAUCIDAE [TEM: *Glaucilla marginata* Bergh, *Glaucus atlanticus* Forster; Light microscopy: *Austraeolis ornata* (Angas)], **AEOLIDIIDAE** [TEM: *Aeolidiella indica* Bergh; Light microscopy: *Aeolidiella alba* Risbec], **FACELINIDAE** [TEM: *Favorinus japonicus* Baba]

Results for *Glaucilla marginata*, *Glaucus atlanticus*, and *Aeolidiella indica* closely agree with those presented above for *Pteraeolidia ianthina*. The acrosomal complex features a small acrosomal vesicle and intertwining of the pedestal with a strongly keeled, short nucleus (Figures 6N–R, 7K). The midpiece shows a single glycogen helix, at least one

secondary helix (anteriorly), and helically organized matrix material (Figure 7J, L). In *Aeolidiella indica*, spermatozoa with two axonemes and two or three glycogen helices were sometimes observed (Figure 7L, M). Such duplication of sperm components is not considered by us as evidence of true sperm dimorphism, but rather it is almost certainly the result of spermiogenic abnormalities.

Favorinus japonicus differs from *Pteraeolidia ianthina*, Glaucidae, and Aeolidiidae principally in having less pronounced overlap between the acrosomal pedestal and nucleus (Figure 8C). The acrosomal vesicle of *Favorinus japonicus* is small (0.07 μm diameter, Figure 8B), the nucleus is strongly keeled (Figure 8A), and the matrix component of the mitochondrial derivative is clearly subdivided into equal-sized, helical tracts (Figure 8D).

FLABELLINIDAE [*Flabellina rubrolineata* (O'Donoghue)]

Spermatozoa of *Flabellina rubrolineata* also show extensive overlap of the pedestal and the nucleus. However, instead of sheathing the anterior region of the nucleus (observed in the Facelinidae, Aeolidiidae, and Glaucidae), the pedestal component of the *Flabellina rubrolineata* acrosomal complex (length 1.8–2.0 μm) is largely contained within a deep, lateral groove of the nucleus (Figure 8E–G). Anteriorly, the pedestal emerges to support an ovoid acrosomal vesicle similar in size (0.09 μm long, 0.7 μm wide) to those occurring in the Aeolidiidae, Facelinidae, and Glaucidae (Figure 8E, inset). *Flabellina rubrolineata* differs from other aeolidoids in possessing a slightly longer nucleus (6.8–7 μm , with only a single keel, Figure 8H), a midpiece without secondary helices (Figure 8I–K), and in the persistence of the axonemal components into the terminal region of the midpiece (Figure 8L). As observed in other aeolidoids, the basal invagination of the nucleus

Figure 5A–L: Figure A–D, *Phyllidiopsis cardinalis*;
Figure E–L, *Phyllidia nobilis*

- Figure 5A. LS acrosomal complex and nuclear apex ($\times 73,000$).
- Figure 5B. LS nuclei and proximal portion of the midpiece ($\times 5,500$).
- Figure 5C. LS showing flexibility of acrosomal pedestal ($\times 54,700$).
- Figure 5D. TS midpiece region, and (arrow) terminal region of spermatozoon ($\times 46,500$).
- Figure 5E. LS through acrosomal complex ($\times 30,000$). Inset: TS of acrosomal pedestal ($\times 42,000$).
- Figure 5F. LS junction of nucleus and midpiece. Subnuclear ring indicated by arrows ($\times 42,000$).
- Figure 5G, H. TS Proximal portion of midpiece ($\times 51,000$).
- Figure 5I. LS detail of midpiece ($\times 40,000$).
- Figure 5J. LS midpiece showing glycogen helix ($\times 27,000$).
- Figure 5K. Oblique TS midpiece showing paracrystalline material ($\times 58,500$).
- Figure 5L. TS showing terminal region of spermatozoa (?annulus, glycogen piece). Nine wedge-shaped components surround the axonemal doublets ($\times 60,000$).

Abbreviations: ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; gh, glycogen helix; M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material.

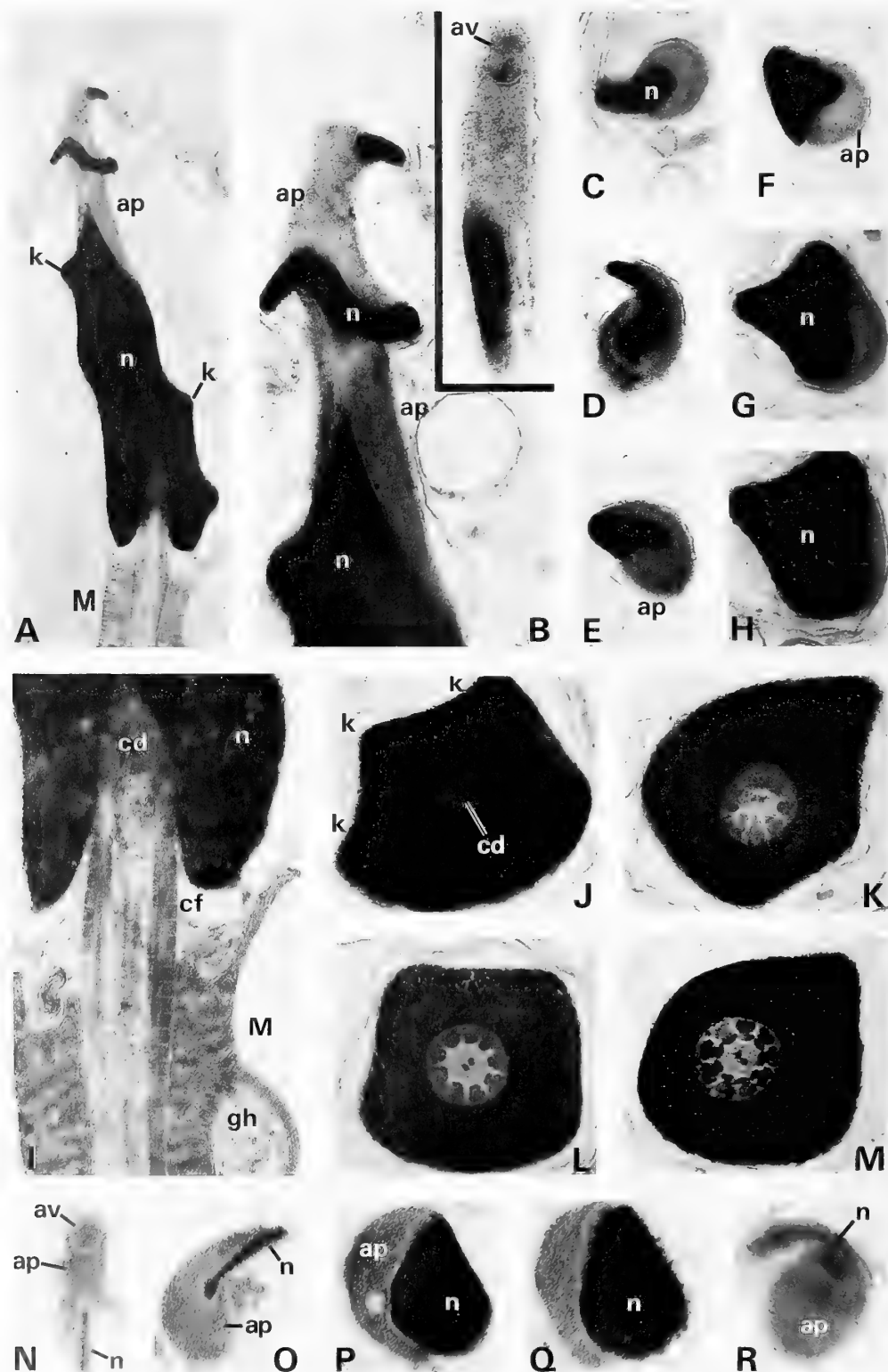


Figure 6A-R: Figure A-M, *Pteraeolidia ianthina*; Figure N-Q, *Glaucilla marginata*; Figure R, *Aeolidiella indica*

Figure 6A. LS acrosomal pedestal, nucleus (with helical keels) and proximal portion of midpiece ($\times 20,000$).

is well developed (depth $0.7\ \mu\text{m}$) with the centriolar derivative, coarse fibers, and distal accessory sheath occupying the invagination (Figure 8I). Figure 8I also shows the presence of a subnuclear ring. Periodicity of banding of the nine coarse fibers (surrounding the axonemal doublets) is $40\ \text{nm}$ in *Flabellina rubrolineata*. Figure 8L shows the only observed longitudinal section (here oblique) of the midpiece-glycogen piece junction in *Flabellina rubrolineata*. Although the entire glycogen piece is not illustrated, the micrograph suggests that the axoneme does not enter this region, and that dense granules (putative glycogen) comprise the bulk of the glycogen piece. The fact that no transverse sections were obtained through the glycogen piece strongly suggests that it comprises a minute proportion of the entire *Flabellina rubrolineata* spermatozoon. The dense collarlike structure shown in Figure 8L is probably a form of annulus.

Mature sperm length in the Aeolidioidea ranges from $160\text{--}170\ \mu\text{m}$ in *Glaucus atlanticus* to $390\text{--}395\ \mu\text{m}$ in *Pteraeolidia ianthina* (for comparison, see Table 1).

DENDRONOTOIDEA

[TEM: LOMANOTIDAE—*Lomanotus vermiformis* Eliot; TEM: HANCOCKIIDAE—*Hancockia* sp.; TRITONIIDAE—TEM: *Marianina rosea* (Provot-Fol); Light microscopy: *Marianina cyanobrachiata* (Rüppell & Leuckart)]

Numerous differences exist between spermatozoa of the three dendronotoidea examined—too many in fact to select a “type” for description.

Acrosomal Complex

In *Lomanotus vermiformis* and *Hancockia* sp., the acrosomal vesicles are large (*Lomanotus vermiformis*— $0.56\ \mu\text{m}$ long, $0.14\ \mu\text{m}$ wide; *Hancockia* sp.— $0.22\ \mu\text{m}$ long, $0.17\ \mu\text{m}$ wide) and set on short ($0.2\text{--}0.25\ \mu\text{m}$ long) wide pedestals at the nuclear apex (Figure 9A–C, F). Whereas the acrosomal vesicle of *Hancockia* sp. is spherical with ho-

mogeneously electron-dense contents (Figure 9F), the vesicle of *Lomanotus vermiformis* is elongate and shows some differentiation of internal contents (enhanced electron density of basal and peripheral areas) (Figure 9A, B). In contrast to *Lomanotus vermiformis* and *Hancockia* sp., the acrosomal complex of *Marianina rosea* consists of a small ovoid acrosomal vesicle ($0.09\ \mu\text{m}$ long, $0.08\ \mu\text{m}$ wide) connected to the finely tapered apex of the nucleus by a minute ($0.1\ \mu\text{m}$ long), wedge-shaped pedestal (Figure 9G, inset).

Nucleus

The fibrous nature of the nucleus in *Lomanotus vermiformis* (Figure 9C) may be the result of osmotic stress, despite the apparently good fixation of other components (see pp. 155, 156 for discussion of this phenomenon in other nudibranchs). Nuclei of *Hancockia* sp. are helically coiled, but show no evidence of helical keels. In contrast, the nucleus of *Marianina rosea* exhibits one major helical keel and two or three minor keels (Figure 9G), and in overall shape resembles nuclei of the Aeolidioidea rather than other Dendronotoidea. The basal invagination in all examined Dendronotoidea is shallow ($0.4\text{--}0.45\ \mu\text{m}$) and occupied by the centriolar derivative (*Lomanotus vermiformis*, Figure 9C) or the centriolar derivative and adjoining portion of the axoneme/coarse-fiber complex (*Marianina rosea*, *Hancockia* sp.—Figure 9I). A subnuclear ring is present in all three dendronotoid species (see Figure 9I).

Midpiece

Aside from the differences in nuclear shape noted above, *Lomanotus vermiformis*, *Hancockia* sp. and *Marianina rosea* also show marked differences in midpiece morphology. In *Lomanotus vermiformis*, the glycogen helix within the immediate post-nuclear region of the midpiece is very well developed, though filled with membranes rather than granular deposits (Figure 9C, D). The glycogen helix in *Hancockia* sp. and *Marianina rosea* is less removed from the main body of the midpiece (Figure 9G, I). *Marianina rosea*

Figure 6B. Detail of pedestal and nucleus of Figure 6A ($\times 43,200$). Inset: acrosomal vesicle supported by pedestal at nuclear apex ($\times 77,000$).

Figure 6C–H. TS anterior-posterior sequence showing intertwining of pedestal and nucleus (C–G $\times 48,000$; H $\times 38,400$).

Figure 6I. LS junction of nucleus and midpiece ($\times 44,000$).

Figure 6J–M. TS anterior to posterior sequence showing structural changes from centriolar derivative to axoneme/coarse-fiber complex. Note helical keels of nucleus ($\times 40,000$).

Figure 6N. LS acrosomal vesicle, portion of pedestal, and nuclear apex ($\times 64,000$).

Figure 6O–Q. TS anterior-posterior sequence showing changes in shape of intertwined pedestal and nucleus ($\times 80,000$).

Figure 6R. TS pedestal and nuclear keel ($\times 60,000$).

Abbreviations: ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; gh, glycogen helix; k, nuclear keels; M, midpiece; n, nucleus.

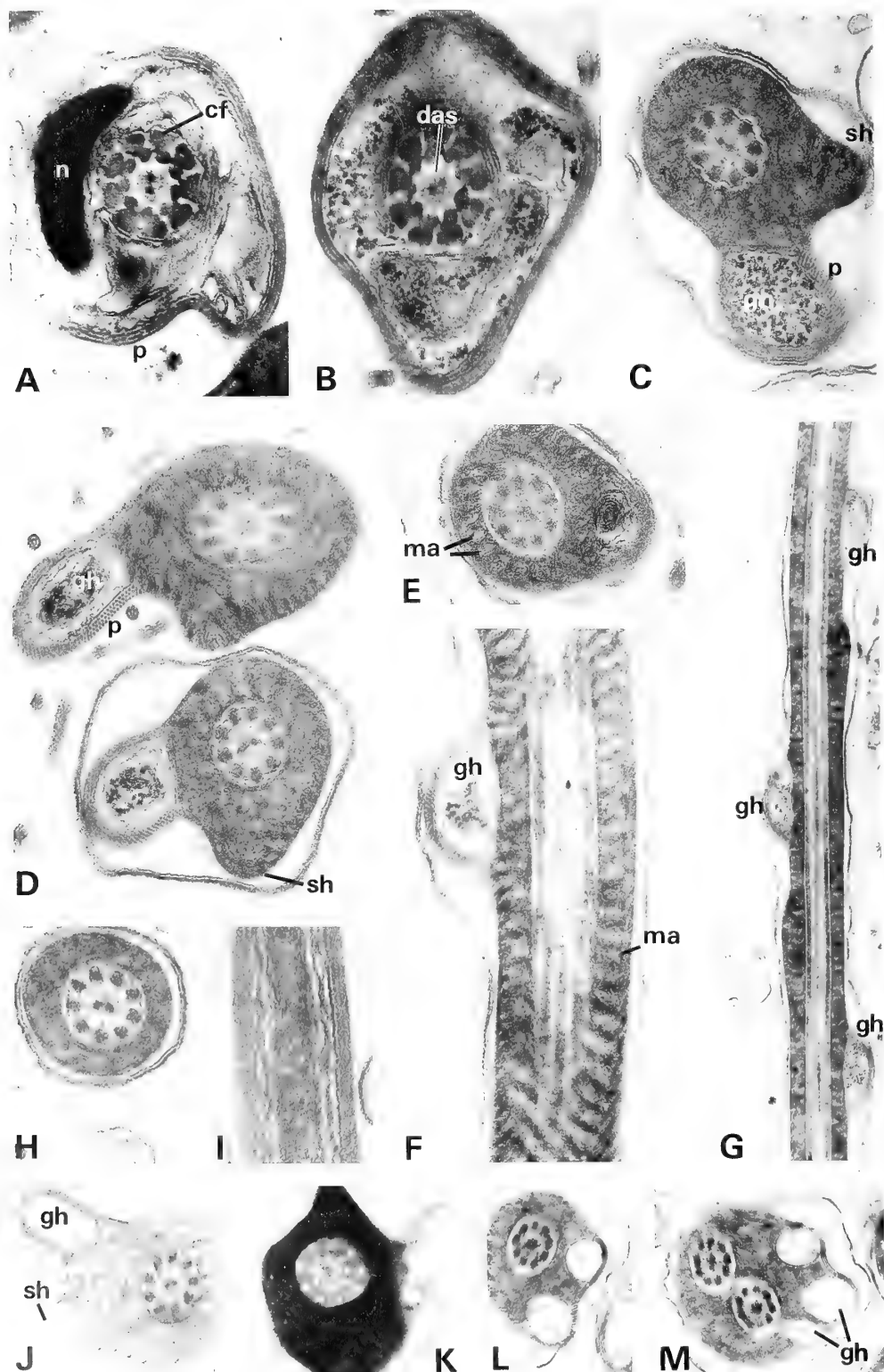


Figure 7A-M: Figure A-I, *Pteraeolidia ianthina*; Figure J-K, *Glaucilla marginata*; Figure L-M, *Aeolidiella indica*

Figure 7A, B. TS neck region of midpiece. Coarse fibers attached to axonemal doublets. Distal accessory sheath envelops central tubules of axoneme ($\times 54,500$).

is also notable in having well defined, helical subdivisions within the matrix material (Figure 9G, I) (also present in *Hancockia* sp. and *Lomanotus vermiformis*, but less apparent). A subnuclear ring was present in all three dendronotoid species studied (for example, Figure 9G).

Glycogen Piece

No information on the midpiece/glycogen-piece junction could be obtained for any of the three dendronotoids studied. In *Lomanotus vermiformis*, however, transverse sections revealed that the axoneme continues intact from the midpiece into the glycogen piece (where it is surrounded by putative glycogen deposits), but soon thereafter degenerates from a 9+2 configuration into singlet microtubules (Figure 9E). Available data for *Lomanotus vermiformis* suggest that the glycogen piece is short, probably less than 2 μm long.

Mature spermatozoa of the Dendronotoidea range from 200–230 μm in *Lomanotus vermiformis* to 320–330 μm in *Marianina rosea*.

ARMINOIDEA

(DORIDOMORPHIDAE—*Doridomorpha gardineri* Eliot;
ARMINIDAE—*Dermatobranchus fortunata* Bergh)

Doridomorpha gardineri

The acrosomal pedestal is 0.36–0.4 μm long, sheaths the tapered apex of the nucleus, and apically, supports a small (0.08 μm long, 0.65 μm wide) acrosomal vesicle (Figure 9J). A small cavity near the base of the pedestal is sometimes observed in longitudinal sections (Figure 9J). The length of the nucleus could not be determined. However, it is circular in transverse profile, and has a moderately deep (0.66 μm) basal invagination which houses the centriolar derivative, distal accessory sheath, and initial portion of the axoneme/coarse-fiber complex (Figure 9L). The distal accessory sheath (length 0.4 μm) is penetrated

by the central microtubules of the axoneme (Figure 9L). Periodicity of primary banding of the coarse fibers is 52 nm. A subnuclear ring is present (Figure 9L).

Within the midpiece, matrix materials are organized into clearly defined helical tracts (Figure 9L). A glycogen helix and secondary helix are present (Figure 9K). Axonemal microtubules persist to the midpiece/glycogen-piece junction, but do not enter the glycogen piece. A simple ring-shaped annulus is present at the junction (Figure 9M). The glycogen piece is 0.4–0.5 μm long and consists of granular deposits and the plasma membrane (Figure 9M).

Dermatobranchus fortunata (not illustrated)

Spermatozoa of this species differ from those of *Doridomorpha gardineri* principally in having more extensive overlap between the acrosomal pedestal and the nucleus and well developed nuclear keels.

Table 2—Summary

Comparative ultrastructural features of nudibranch spermatozoa examined in this study are listed in Table 2, and whole sperm lengths are given in Table 1.

DISCUSSION

Nudibranch Spermatozoa: Comparison With Other Gastropods

Spermatozoan morphology varies widely within the Gastropoda. In the Prosobranchia, for example, spermatozoa may be comparatively simple in structure (*e.g.*, externally fertilizing archaeogastropods) or complex and often dimorphic (most internally fertilizing groups such as Neritimorpha, Caenogastropoda) (FRANZÉN, 1955; NISHIWAKI, 1964; GIUSTI & SELMI, 1982; KOHNERT & STORCH, 1984; KOIKE, 1985; HEALY, 1988a).

Figure 7C, D. TS proximal region of midpiece. Note secondary helix, and at top, spermatozoon without investing plasma or mitochondrial membranes ($\times 46,400$).

Figure 7E. TS middle region of midpiece ($\times 48,000$).

Figure 7F. LS middle region of midpiece ($\times 48,000$).

Figure 7G. LS near proximal region of midpiece ($\times 20,000$).

Figure 7H. TS distal region of midpiece ($\times 52,000$).

Figure 7I. LS terminal region of midpiece (axoneme replaced by dense granules) ($\times 48,000$).

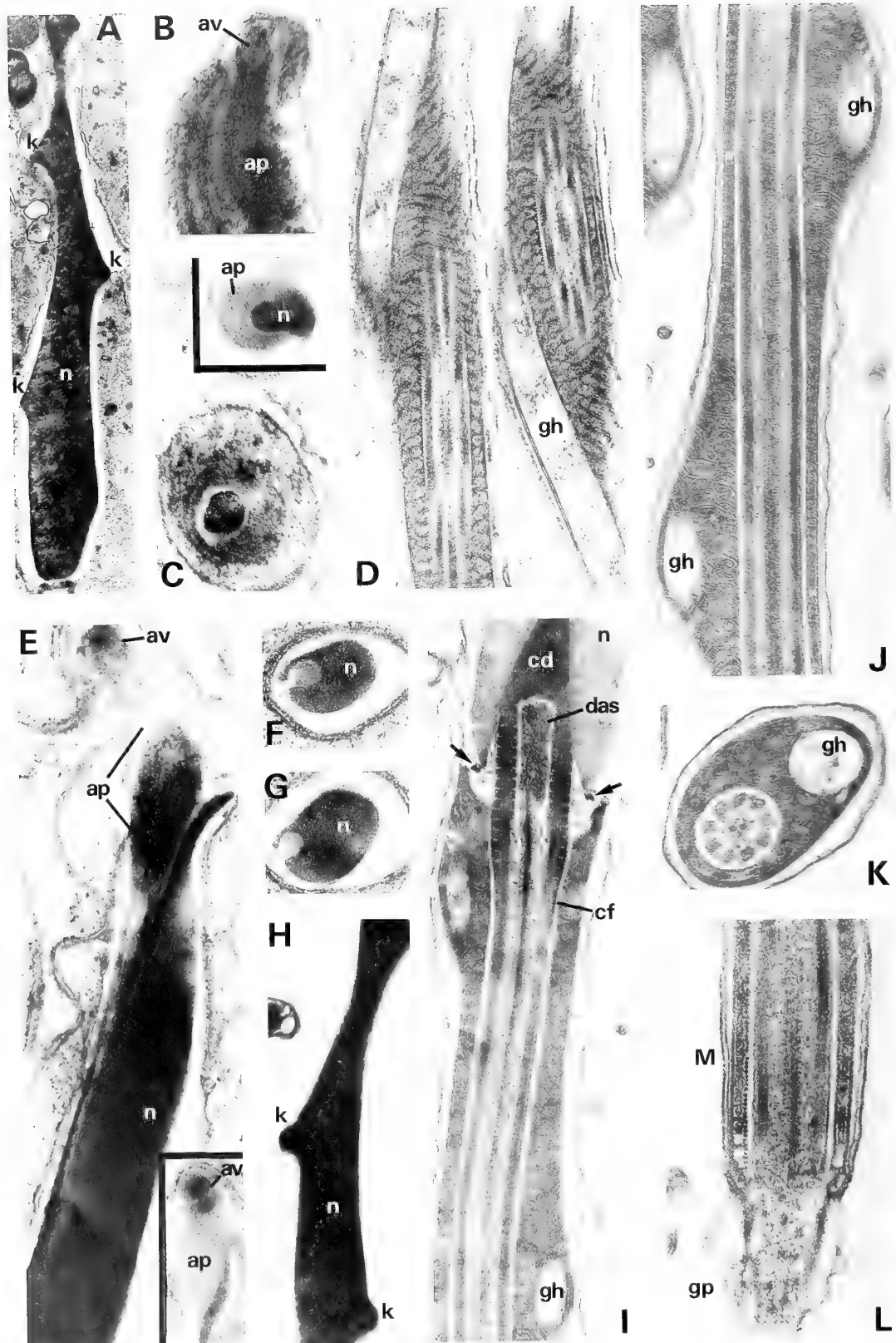
Figure 7J. TS midpiece ($\times 32,000$).

Figure 7K. TS base of nucleus ($\times 32,000$).

Figure 7L. TS midpiece with two glycogen helices ($\times 24,000$).

Figure 7M. TS biaxonemal spermatozoon with three glycogen helices ($\times 24,000$).

Abbreviations: cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; ma, matrix material; n, nucleus; p, paracrystalline material; sh, secondary helix.



Spermatozoa of the Nudibranchia clearly show all the features of other opisthobranch and pulmonate spermatozoa outlined by HEALY (1983, 1988a), namely a distinctive form of acrosomal complex (round/oblong acrosomal vesicle plus a column-shaped pedestal), a nucleus (usually with one or more helical keels), and a complex midpiece (mitochondrial derivative enclosing axoneme, coarse fibers, and at least one glycogen-filled helix) (summarized in Figure 10A-E).

The neck region of nudibranch spermatozoa, like that observed in most other heterobranchs, features a pluglike centriolar derivative continuous with the banded coarse fibers and the axoneme, a distal accessory sheath, and subnuclear ring (Figure 10D). Similarly, the helical mitochondrial derivative, with its lattice-like paracrystalline layers and enclosed axoneme, coarse fibers, and glycogen helix, is essentially as observed in other heterobranch spermatozoa (Figure 10B, E) (for comparison see ANDERSON & PERSONNE, 1967, 1976; OHSAKO, 1971; THOMPSON, 1973; RITTER & ANDRE, 1975; KITAJIMA & PARAENSE, 1976; MAXWELL, 1976, 1980; DAN & TAKAICHI, 1979; ATKINSON, 1982; REGER & FITZGERALD, 1982; HEALY, 1983, 1986, 1988a, b; HEALY & WILLAN, 1984; HEALY & JAMIESON, 1989; SUMIKAWA & FUNAKOSHI, 1984; SELMI *et al.*, 1988). Although spermatozoa of nudibranchs consistently show poor development of the glycogen piece (absent in some taxa: for comparison see Figure 10K-N), this has previously been demonstrated in the Notaspidea (HEALY & WILLAN, 1984), Pyramidelloidea (HEALY, 1988b) and Anaspidea (HEALY, 1984). Enclosure of substantial glycogen

deposits within the mitochondrial derivative may obviate the need for a well-developed glycogen piece (THOMPSON, 1973; HEALY & WILLAN, 1984; see also MAXWELL, 1980, for discussion of glycogen in heterobranch spermatozoa). Absence of the midpiece membranes in some nudibranchs (for example in some spermatozoa of *Pteraeolidia ianthina*, herein) has been noted previously in aplysiids (BEEMAN, 1973, loss of plasma membrane only) and in basommatophorans (ACKERSON & KOEHLER, 1977, loss of plasma and mitochondrial membranes). Such membrane loss could be a normal maturational or capacitational phenomenon (BEEMAN, 1973; ACKERSON & KOEHLER, 1977), or the result of imperfect cell fixation. Further work on membrane substructure and function in heterobranch spermatozoa seems necessary in order to clarify this issue.

In summary, it was surprising that the present study failed to find sperm components that were new or specifically restricted to the Nudibranchia.

Autosperm and Allosperm

In the present study we have examined only the autosperm (*i.e.*, endogenous sperm) of each species (either those occurring in the ovotestis or the hermaphrodite duct and ampulla). Work by THOMPSON (1966, 1973) on allosperm (*i.e.*, exogenous sperm) of *Archidoris pseudoargus* and more recently by MEDINA *et al.* (1988b) on allosperm of *Hyphselodoris messinensis* (Ihering) has demonstrated that, at least within the receptaculum seminis, no noticeable changes in the ultrastructure of sperm components have taken place after sperm transfer (acrosomal complex, nucleus, and

Figure 8A-L: Figure A-D, *Favorinus japonicus*; Figure E-L, *Flabellina rubrolineata*

Figure 8A. LS nucleus (note keel) and proximal portion of midpiece ($\times 14,200$).

Figure 8B. LS showing acrosomal vesicle and apex of pedestal of immature spermatozoon (acrosomal complex still associated with support structures). ($\times 63,000$).

Figure 8C. TS through posterior region of pedestal of immature sperm ($\times 63,000$). Inset: TS through pedestal and nucleus of mature spermatozoon ($\times 63,000$).

Figure 8D. LS midpiece showing helical subdivision of matrix material ($\times 30,000$).

Figure 8E. LS acrosomal complex and nuclear apex. Note that the posterior portion of the pedestal is inserted into a deep nuclear invagination. Inset: acrosomal vesicle and tip of pedestal ($\times 60,000$).

Figure 8F, G. TS showing enclosure of acrosomal pedestal in nuclear groove ($\times 65,250$).

Figure 8H. LS posterior portion of nucleus, showing keel ($\times 20,200$).

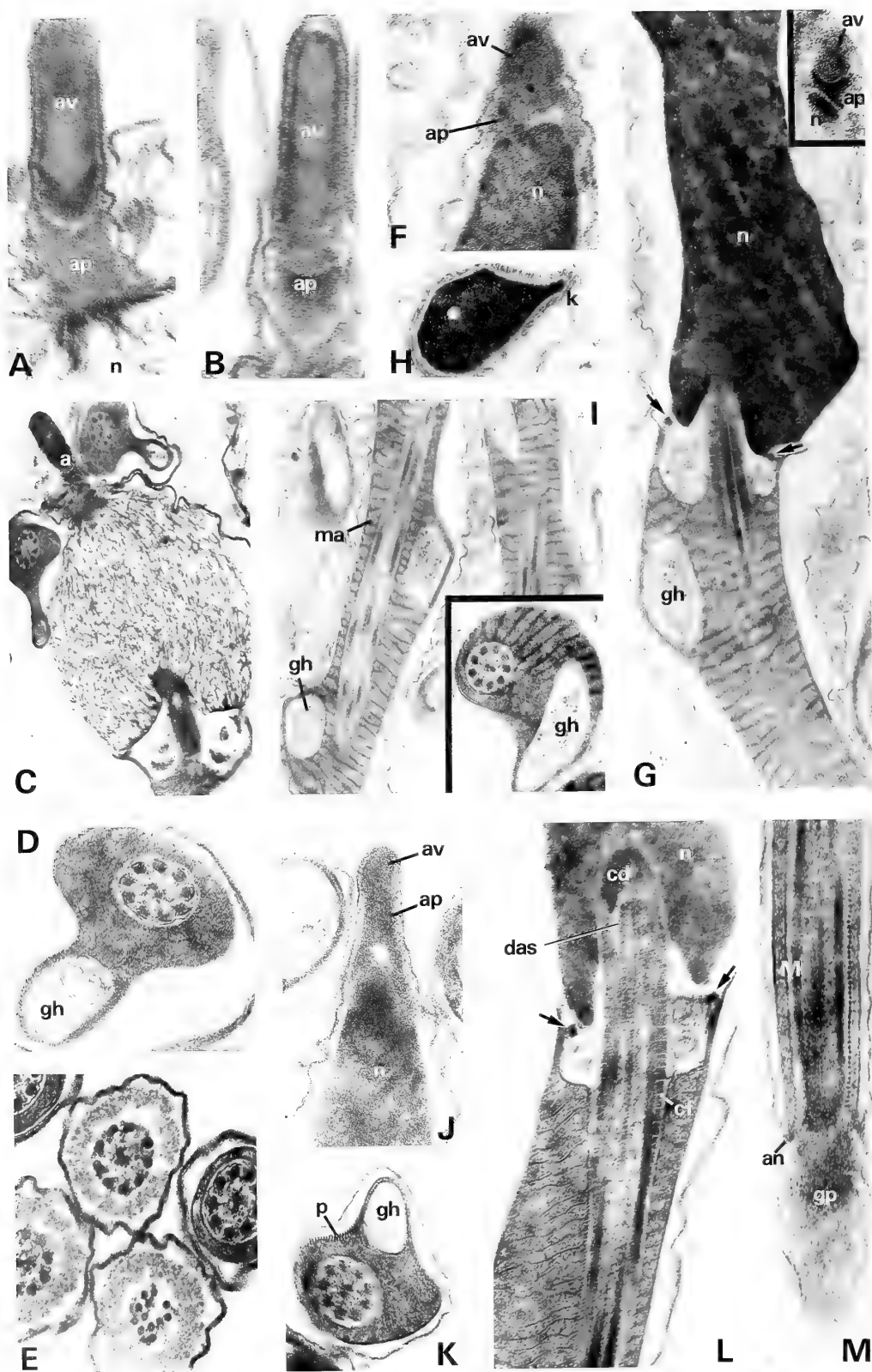
Figure 8I. LS junction of nucleus and midpiece. Subnuclear ring indicated by arrows ($\times 38,250$).

Figure 8J. LS midpiece ($\times 36,500$).

Figure 8K. TS midpiece ($\times 50,250$).

Figure 8L. LS junction of terminal portion of midpiece and glycogen piece ($\times 54,700$).

Abbreviations: ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; k, nuclear keel; M, midpiece; n, nucleus.



midpiece still intact). Spermatozoa within the bursa copulatrix, however, are always degenerate (THOMPSON, 1966; SCHMEKEL, 1971; MEDINA *et al.*, 1988a). HOLMAN (1972) reported that the reacted acrosome of *Acanthodoris pilosa* (Müller) (allosperm) was characterized by rolled back membranes and an "expanded" form. Unfortunately no micrographs were provided by Holman to support this observation. To our knowledge the acrosome reaction remains to be demonstrated in auto- and allosperm of heterobranch gastropods. In the present study we noted in a number of species that spermatozoa taken from the hermaphrodite duct had nuclei that were clearly fibrous in substructure and often inflated in shape (*e.g.*, *Hexabran- chus sanguineus*, *Asteronotus cespitosus*, *Kaloplocamus yatesi*, *Rostanga arbutus*), whereas mature or almost mature sperm nuclei from the ovotestis of the same animals were condensed and uniformly electron-dense. Although we assumed at first that this may be due to fixative osmolarity, fibrous nuclei only occurred in certain species within each processing run (phyllidiids and most aeolidoids, for example, were not affected), and other sperm components showed little evidence of osmotic stress. Previous authors, employing a range of fixation schedules, have demonstrated the same phenomenon in other nudibranchs (SCHMEKEL, 1971; HOLMAN, 1972; THOMPSON, 1966, 1973; MEDINA *et al.*, 1988b), in cephalaspids (THOMPSON, 1973; HEALY unpublished) and in onchidiid and siphonariid pulmonates (HEALY, 1983, 1986; SUMIKAWA & FUNAKOSHI, 1984; AZEVEDO & CORRAL, 1985; SELMI *et al.*, 1988). A full expla-

nation as to why fibrous sperm nuclei occur in these euthyneuran gastropods has yet to be advanced. AZEVEDO & CORRAL (1985) suggest that complete dehydration of sperm nuclei of *Siphonaria algesirae* Quoy & Gaimard may not be a prerequisite for gamete maturation. However, it has been shown that immature (testicular) sperm nuclei of other siphonariids and nudibranchs are fully condensed (see Figures of HEALY, 1983; MEDINA *et al.*, 1988b; this account). MEDINA *et al.* (1988b) refer to the fibrous (ma- ture) nuclei of *Hypselodoris messinensis* as "decondensed," but could not offer any functional reason for the phenom- enon. SELMI *et al.* (1988) have suggested that this condition, as observed by them in *Onchidiella celtica* (Cuvier), could prove to be due to low levels of protamines in mature sperm nuclei, or may even be an expression of sperm dimorphism. It is possible that pH may also be involved in changes in nuclear substructure. HOLMAN (1972), for example, observed that short periods of motility (2–5 min) could sometimes be induced in allosperm of *Acanthodoris pilosa* by exposure to alkaline seawater. During motility the sperm "head" became swollen, then the tail detached. Significantly no structural changes were observed in au- tospERM (all non-motile) subjected to the same treatment. Holman concluded that autosperm and allosperm of *Acan- thodoris pilosa* may differ physiologically, and possibly may show structural differences in permeability of the plasma membrane. Clearly much cytochemical work needs to be carried out to determine the true cause of fibrous sperm nuclei in nudibranchs and other heterobranch gastropods.

Figure 9A–M: Figure A–E, *Lomanotus vermiformis*; Figure F, G, *Hancockia* sp.;

Figure H, I, *Marianina rosea*; Figure J–M, *Doridomorpha gardineri*

Figure 9A, B. LS acrosomal complex and nuclear apex ($\times 56,000$).

Figure 9C. LS showing acrosomal complex, nucleus (fibrous, inflated), and initial region of mid- piece. TS of midpieces also visible ($\times 18,000$).

Figure 9D. TS proximal portion of midpiece. Note positioning of glycogen helix ($\times 47,250$).

Figure 9E. TS through terminal region of midpiece (at right) and glycogen piece (with intact axoneme, and with axoneme reduced to singlet microtubules) ($\times 45,500$).

Figure 9F. LS acrosomal complex and nuclear apex ($\times 40,000$).

Figure 9G. Junction of nucleus and midpiece. Arrows indicate subnuclear ring ($\times 26,000$). Inset: LS acrosomal complex and nuclear apex ($\times 55,300$).

Figure 9H. TS nucleus of slightly immature spermatozoon showing keel ($\times 28,700$).

Figure 9I. LS anterior region of midpiece showing helical subdivisions of matrix ($\times 21,000$). Inset: TS of midpiece ($\times 28,000$).

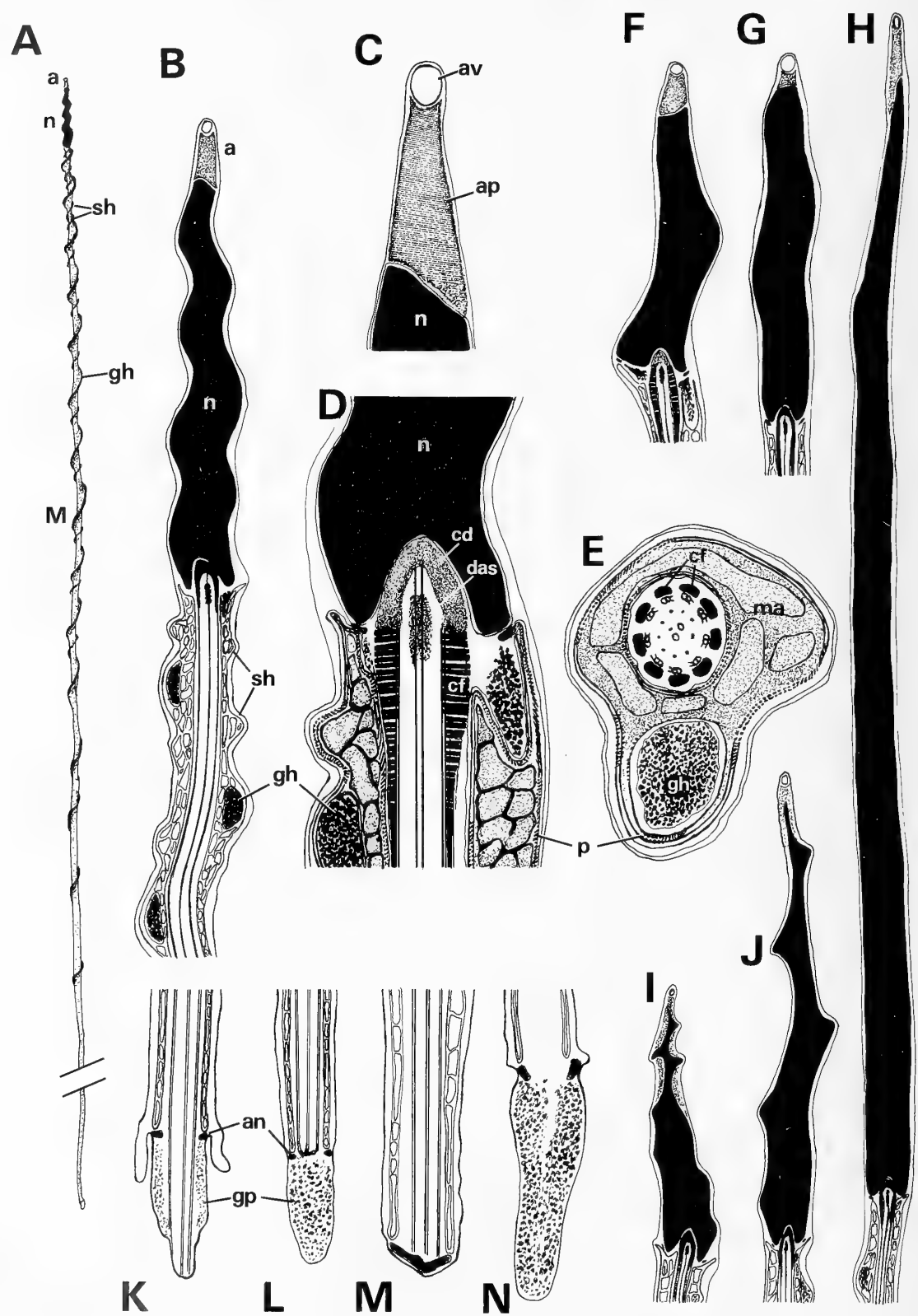
Figure 9J. LS acrosomal complex and nuclear apex ($\times 56,000$).

Figure 9K. TS midpiece ($\times 40,000$).

Figure 9L. LS junction of nucleus and midpiece. Subnuclear ring indicated by arrows ($\times 40,400$).

Figure 9M. LS junction of midpiece and glycogen piece ($\times 53,000$).

Abbreviations: a, acrosomal complex; an, annulus; ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; k, nuclear keel (s); M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material.



Sperm Dimorphism

ROGINSKAYA (1964) reported dimorphic sperm nuclei in seven species of *Coryphella* (= *Flabellina sensu* MILLER, 1971) from the White, Barents, and Okhotsk seas (*C. rufibranchialis* Johnston, *C. fusca* O'Donoghue, *C. athadona* Bergh, and four unnamed species), but only a single type of sperm nucleus in 21 other nudibranch species (representing the Doridoidea, Dendronotoidea, and other species of Aeolidioidea). Sperm nuclei of the seven *Coryphella* species were found to be either short and curved (referred to as "typical sperm" by ROGINSKAYA, 1964) or long and helically coiled (referred to as "atypical sperm"). Both types of nucleus reacted positively to nuclear stains (Feulgen, Heidenhain's iron hematoxylin). According to Roginskaya, only "typical" sperm are transferred during copulation, while "atypical" sperm are retained within penis indicating that "atypical" sperm are not involved in fertilization. Roginskaya also examined spermatozoa of other genera of the Flabellinidae (*Flabellina*, *Chlamylla*) but only found a single type of spermatozoon, and concluded that sperm dimorphism in *Coryphella* supported the need for a separate family for this genus (i.e., Coryphellidae as distinct from Flabellinidae). Unfortunately this work has never been followed up using electron microscopy. SCHMEKEL (1971) included some TEM micrographs of ovotestis sperm from *Coryphella pedata* (Montague) in her review of nudibranch reproductive systems, but was evidently unaware of ROGINSKAYA's (1964) work and its significance. Her published micrographs, however, while not providing any ultrastructural evidence to support sperm dimorphism in *Coryphella*, do help to establish that sper-

matozoa of *Coryphella* are very similar to those of *Flabellina*. Our work on *Flabellina rubrolineata* indicates only a single type of sperm in this species, which is consistent with Roginskaya's light microscopic observations on *Flabellinopsis iodinea* (Cooper).

Aside from THOMPSON's (1973) light microscopic observation that the acrosomes of *Dendronotus iris* Cooper may be either straight or helical, and ROGINSKAYA's (1964) findings (discussed above), we are unaware of any other reported incidence of sperm dimorphism in the Nudibranchia. Rare biaxonemal spermatozoa showing multiple glycogen helices such as we have demonstrated for *Aeolidiella indica* (see Figure 7M) are probably products of abnormal spermiogenesis and not examples of true sperm dimorphism. Certainly the profound structural dimorphism observed in spermatozoa of internally fertilizing prosobranchs (for recent reviews see GIUSTI & SELMI, 1982; HEALY, 1988a) is not encountered in the Nudibranchia or any other group of heterobranch gastropods.

Comparisons Within the Nudibranchia

Results of our comparative study support THOMPSON's (1973) statement that despite similarities in general morphology, spermatozoa of nudibranchs do show marked variation among taxa in the shape, substructure, and size of the acrosome (vesicle and pedestal components) (Figure 11). This study also reveals notable differences among genera and families in the shape of the nucleus (short or long, keeled or lacking keels, variation in depth of basal invagination), the spatial relationship of the acrosomal pedestal with the nucleus (distinct, overlapping, inserted

Figure 10 A–N. Summary of sperm ultrastructural features in the Nudibranchia

Figure 10A–E: *Chromodoris annae*.

Figure 10A. Positioning of the acrosomal complex, nucleus, midpiece (here greatly shortened), and terminal region ($\times 1,750$).

Figure 10B. Acrosomal complex, nucleus, and proximal region of midpiece ($\times 12,000$).

Figure 10C. Detail of acrosomal complex and nuclear apex ($\times 40,000$).

Figure 10D. Detail of nucleus-midpiece junction ($\times 40,000$).

Figure 10E. TS midpiece showing distribution and organization of paracrystalline and matrix components and glycogen helix ($\times 60,000$).

Figure 10F–J. Morphological variation in nudibranch sperm nuclei (F, *Rostanga arbutus*; G, *Sclerodoris* cf. *apiculata*; H, *Phyllidiopsis cardinalis*; I, *Pteraeolidia ianthina*; J, *Favorinus japonicus*) ($\times 12,000$).

Figure 10K–N. Morphological variation in the midpiece-glycogen piece junction in nudibranch sperm (K, *Doriopsis granulosa*; L, *Doridomorpha gardineri*; M, *Chromodoris annae* (dense cap may be modified annulus); N, *Jorunna pantherina*) ($\times 35,000$).

Abbreviations: a, acrosomal complex; an, annulus; ap, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibers; das, distal accessory sheath; gh, glycogen helix; gp, glycogen piece; M, midpiece; ma, matrix material; n, nucleus; p, paracrystalline material; sh, secondary helices.

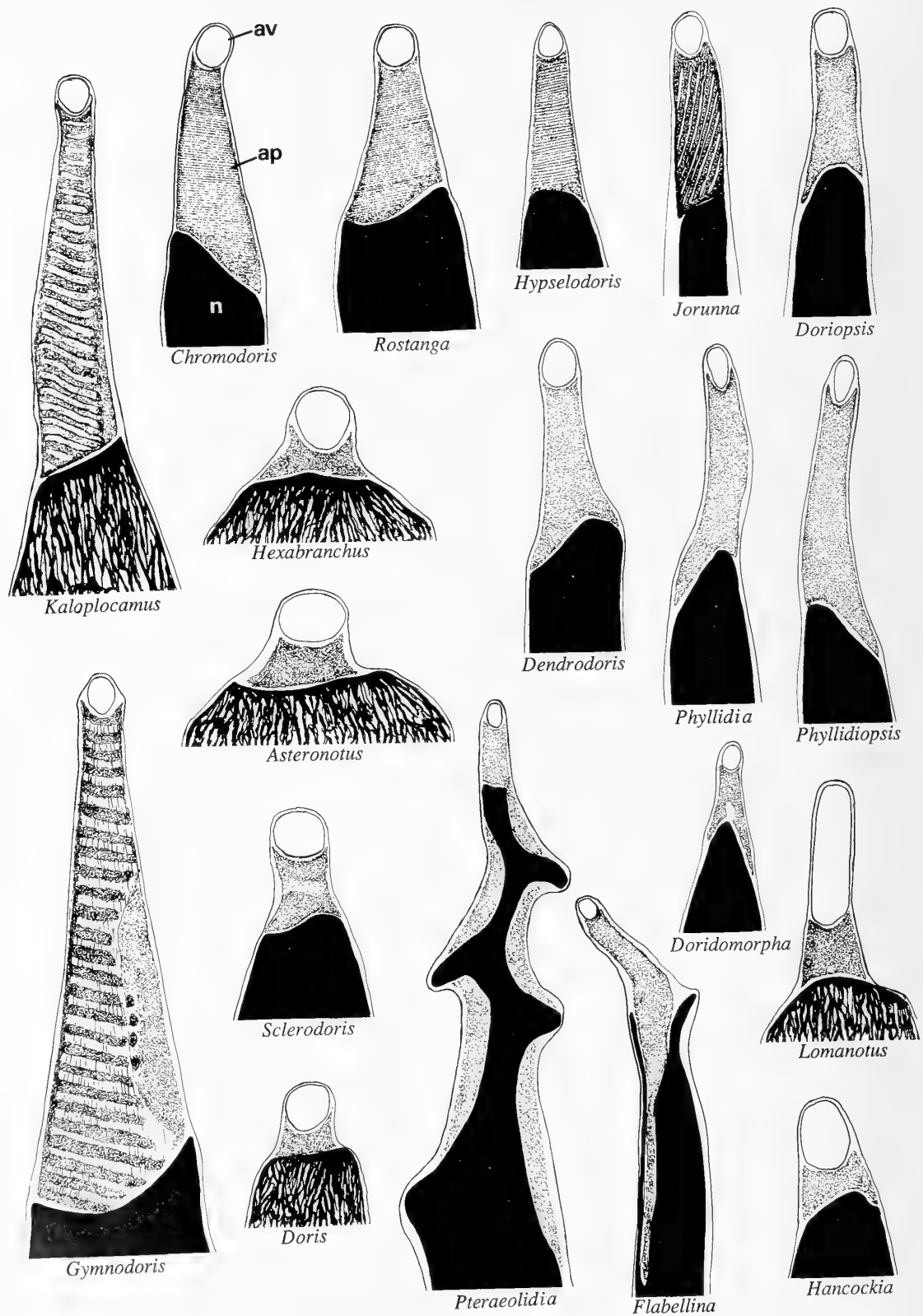


Figure 11

Comparative morphology of the acrosomal complex in the Nudibranchia (all $\times 40,000$). Abbreviations: ap, acrosomal pedestal; av, acrosomal vesicle; n, nucleus.

or intertwined), organization of the midpiece (secondary helices present or absent, shape of glycogen helix, organization of matrix component), and the morphology of the glycogen piece (distribution of granules, presence or absence of axonemal microtubules, shape of annulus) (Figure 10F–N).

Unfortunately we could not find any sperm features that clearly defined the Nudibranchia. Within the order, however, spermatozoa provide information that may help in the determination of relationships among genera, families, and possibly superfamilies.

Acrosomal Complex and Nucleus

Morphology of the acrosomal complex and nucleus appears to be consistent within genera and/or families, although at the superfamily level it is sometimes impossible to identify features diagnostic of a particular group (e.g., the Doridoidea) (Figures 10F–J, 11).

The Aeolidioidea show pronounced overlap between the acrosomal pedestal and the nucleus (achieved by intertwining in the Glaucidae, Facelinidae, and Aeolidiidae, and by insertion of the pedestal in a long nuclear groove in the Flabellinidae) as well as a small, spherical acrosomal vesicle.

The Arminoidea (*Doridomorpha gardineri*) also possess a small, spherical acrosomal vesicle, but the degree of pedestal overlap with the nucleus in this species is no greater than that occurring in many Doridoidea.

Marked variation in the size and shape of the acrosomal complex occurs in the Dendronotoidea. The large size of the acrosomal vesicle in *Lomanotus vermiformis* and *Hancockia* sp. suggests a connection between the Dendronotoidea and Doridoidea. *Marianina rosea*, in contrast, shows nuclear and acrosomal features more consistent with those of the Aeolidioidea than other Dendronotoidea. Clearly there is a need for additional information on the spermatozoa of Dendronotoidea, particularly the Dendronotidae (one species of which reputedly shows dimorphic acrosomal morphology [*Dendronotus iris*—see THOMPSON, 1973]) and the Tritoniidae.

The Doridoidea show remarkable variation between taxa in the structure of the acrosomal complex, nucleus, and glycogen piece (Figures 10, 11). Two basic types of acrosomal morphology can be recognized within this superfamily: (1) large acrosomal vesicle set on a short, squat pedestal, with nil or slight overlap between pedestal and nucleus (*Hexabranhus sanguineus*, *Doris verrucosa*, *Asteronotus cespitosus*, *Sclerodoris* cf. *apiculata*) and (2) medium-sized acrosomal vesicle set on a tapered pedestal, with marked overlap between pedestal and nucleus (all other investigated Doridoidea) (Figure 11). Within the second category, pedestal substructure and length are variable. In *Chromodoris* spp., *Rostanga arbutus* (this account), and *Hypselodoris* spp. (MEDINA *et al.*, 1988a, b), the pedestal shows fine striations. Pedestals of *Kaloplocamus yatesi* (Polyceridae) and *Gymnodoris* sp. (Gymnodorididae) are remarkable in their pronounced length (longer than all

other nudibranchs) and coarsely banded substructure—features that suggest close affinities between the Gymnodorididae and Polyceridae. In the Phyllidiidae, the acrosomal vesicle is oblong rather than spherical, and the pedestal is slender. Phyllidiid spermatozoa differ from other Doridoidea in possessing a moderately long, straight nucleus (twice to four times the length of most other dorid nuclei, Figure 10). Sperm nuclei of *Doriopsis granulosa* are also long (12–15 μ m) but are helically coiled (like other Doridoidea).

Aside from reflecting systematic relationships, the observed variations in the size of the acrosomal vesicle and length/shape of the pedestal within the Doridoidea are probably also connected with egg morphology (size, yolk content, width of vitelline layer). We cannot, at this stage, confirm any structural correlation between nudibranch sperm and eggs, but note that FRANZÉN (1983) has found a positive correlation between nuclear elongation and yolky eggs in the Bivalvia.

Neck Region, Midpiece

Most variation in the neck region (nucleus-midpiece junction) of nudibranch spermatozoa centers on the depth of the basal invagination of the nucleus. This invagination is relatively deeper in the Aeolidioidea than in other nudibranchs, with the axoneme/coarse-fiber complex intruding into the nuclear invagination. In contrast, the axoneme/coarse-fiber complex of some Doridoidea (e.g., *Kaloplocamus yatesi*, *Lomanotus vermiformis*, *Gymnodoris* sp.) commences outside the poorly developed nuclear invagination.

The midpiece, which forms the bulk of the nudibranch spermatozoon, is extremely variable in length, ranging from 125 μ m in *Miamira magnifica* to a maximum of 590–615 μ m in *Doriopsilla miniata*. It is interesting to note that midpiece and total sperm length vary even within well defined genera (see Table 1, and THOMPSON, 1973). Sperm or midpiece length may eventually prove useful in resolving problems of species identification, particularly in cases of disputed species status. At the ultrastructural level, the mitochondrial derivative may show one or sometimes two secondary helices in addition to the single glycogen helix incorporated within the derivative. Previously it was believed that nudibranch spermatozoa may universally lack secondary keels (see THOMPSON, 1973; MAXWELL, 1983). Helical subdivision of the matrix component of the derivative is most pronounced in the Aeolidioidea, Arminoidea, and Dendronotoidea, taking the form of well defined tracts. In the Doridoidea, the helical orientation of the matrix is often obscured, though clearly showing compartmentalized substructure.

Glycogen Piece, Annulus

In all nudibranch species examined at the TEM level, the glycogen piece is either poorly developed or possibly absent (see Figure 10K–N). The axoneme may terminate

within the midpiece or persist into the glycogen piece. Only in *Doriopsis granulosa* does the axoneme form the posterior tip of the spermatozoon (Figure 10K). Most commonly the annulus is a simple electron-dense ring associated with the inner surface of the plasma and mitochondrial membranes at the midpiece/glycogen-piece junction. The cap-shaped structure forming the terminal tip of some nudibranch spermatozoa (e.g., *Chromodoris annae*, *Tambja* cf. *oliva*—see Figure 10) may represent a modified annulus.

Taxonomic and Phylogenetic Considerations

Although the present study failed to find sperm characters that specifically define the Nudibranchia, the data obtained do permit some evaluation of existing views on the origins of the group and possible relationships within and between the four superfamilies. We wish to stress, however, that numerous nudibranch taxa remain to be examined and, for this reason, a cladistic analysis of the Nudibranchia using sperm features is not attempted here. Inevitably as more spermatological information becomes available, a clearer pattern of relationships within the Nudibranchia should emerge.

On the basis of general anatomy, modern authors hold that the Dendronotoidea, Arminoidea and Aeolidioidea, as a group (Cladobranchia), differ markedly from the Doridoidea (Anthobranchia). MINICHEV (1970) considered that anatomical differences between the Doridoidea and the remainder of the Nudibranchia were great enough to suggest independent origins for both groups. SCHMEKEL (1985: 252–253), however, has argued that despite anatomical differences between the Anthobranchia and the Cladobranchia, these two groups are linked by significant apomorphies (13 chromosome pairs, concentrated nervous system, loss of albumen gland, presence of cells with “special vacuoles”) thereby suggesting a common origin for all nudibranchs probably from a pleurobranch-like notaspide. Most recently WILLAN (1987) has reviewed the anatomy, classification, and phylogeny of the Notaspidea. He concluded that the Notaspidea probably shared a common cephalaspide ancestry with anthobranch nudibranchs rather than directly giving rise to them.

Existing sperm data are at least consistent with the view that the Nudibranchia (herein; THOMPSON, 1973; MEDINA *et al.*, 1985–1988) are closely allied to pleurobranch notaspids (ODHNER, 1939; GHISELIN, 1966; THOMPSON, 1973; GOSLINER & GHISELIN, 1984; HEALY & WILLAN, 1984). So few cephalaspide taxa have been examined for sperm ultrastructure (*Acteon tornatilis*—THOMPSON, 1973; *Haminoea simillima* Pease, *Philine angasi* Crosse & Fischer, *Tornatina* sp.—HEALY, 1982a, 1984) that at present it is impossible to evaluate WILLAN's (1987) hypothesis of a cephalaspide origin for the Notaspidea and Anthobranchia. Certainly there is no sperm evidence to reject this proposal. Given the specialized features of *Umbraculum sinicum* (Gmelin) spermatozoa (featuring complex intertwining of nucleus and mitochondrial derivative—THOMPSON, 1973;

HEALY & WILLAN, 1984) it seems highly unlikely that the Umbraculidae are ancestral to the Nudibranchia as suggested by BOETTGER (1954). Nevertheless a study of *Tylodina* (Tylodiniidae) will be necessary to determine whether spermatozoa of the entire superfamily Tylodinoidea are as specialized as those of *Umbraculum sinicum*.

Interestingly, sperm data do lend some support to BOETTGER's (1954) association of the Dendronotoidea with the Doridoidea rather than with the Arminoidea and Aeolidioidea. Spermatozoa of examined species of Dendronotoidea (species of Hancockiidae, Lomanotidae, and Tritoniidae [Marianinae]) showed marked variation in the size and shape of the acrosomal vesicle and pedestal: *Marianina rosea* has a very small acrosomal vesicle (similar in size to those of Aeolidioidea and Arminoidea) while in *Hancockia* sp. and *Lomanotus vermiformis* the vesicle is well developed (similar to Doridoidea). Given that the Dendronotoidea are universally regarded as a monophyletic group (united by the presence of tubular rhinophoral sheaths—WILLAN, 1988), acrosomal morphology in the three dendronotoids examined may reflect family level differences. Further investigations of sperm ultrastructure should be directed towards larger, more “typical” dendronotoids (e.g., species of *Dendronotus*), particularly since the three species included in this study are advanced, aeolidiform animals.

Within the superfamilies, the Doridoidea seem to be divisible into four groups on the basis of acrosomal and nuclear features: (1) Chromodorididae (*Chromodoris* spp.), some Dorididae (*Jorunna pantherina*, *Rostanga arbutus*, *Hypselodoris* spp.), Dendrodorididae (*Dendrodoris nigra*); (2) Gymnodorididae (*Gymnodoris* sp.), Polyceridae (*Kaloplocamus yatesi*); (3) Dorididae (*Doris verrucosa*, *Asteronotus cespitosus*, *Sclerodoris* cf. *apiculata*), Hexabranchidae (*Hexabranchius sanguineus*); and (4) Phyllidiidae (*Phyllidia* spp., *Phyllidiopsis* spp.). If the more prevalent, group 1 acrosomal complex is ancestral for the Doridoidea, then two trends are apparent: one towards an increase in vesicle size and a decrease in pedestal length (group 3) and another towards a decrease in vesicle size and an increase in pedestal length (group 4, correlated with a substantial increase in nuclear length). On the basis of our data, there are no compelling reasons to associate the Dendrodorididae with the Phyllidiidae (as Porostomata—see SCHMEKEL, 1985). The long, coarsely banded pedestals of group 2 (Gymnodorididae and *Kaloplocamus yatesi* of the Polyceridae) could be derived readily from a group 1 pedestal (which often shows fine striations). Much additional data are needed for the Doridoidea, particularly the more primitive families and genera (e.g., *Bathydoris*).

The Aeolidioidea can be divided into two groups on the basis of sperm morphology: (1) Flabellinidae; and (2) Facelinidae, Glaucidae, Aeolidiidae. These groups correlate with the two major branches of the heteroproct Aeolidioidea recognized by SCHMEKEL (1985) (1—Piseinoteciidae + Flabellinidae; 2—Facelinidae + Aeolidiidae). Absence of sperm data makes it impossible to comment on the relationship between acleioproct aeolidioideans and the

Heteroprocta, or the view expressed by some authors (e.g., GHISELIN, 1966) that the Aeolidioidea may be polyphyletic. ROGINSKAYA's (1964) report of sperm dimorphism in *Coryphella* (seven out of seven examined species) has already been mentioned (see "Sperm Dimorphism," above). If this finding, unique among the Nudibranchia, can be substantiated at the ultrastructural level, then familial status for the genus would seem justified (favored by ROGINSKAYA, 1964). If it cannot be confirmed, then the demonstrated similarity of *Coryphella* sperm (*C. pedata*—see micrographs of SCHMEKEL, 1971) to sperm of *Flabellina* (*F. rubrolineata*) would support the currently accepted placement of *Coryphella* within the Flabellinidae. We believe that examination of sperm ultrastructure in *Babakina* may help determine the correct family placement of this genus (for differing views on the position of *Babakina* see MILLER, 1974; GOSLINER, 1980).

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Acochlidium fijiensis sp. nov.
(Gastropoda: Opisthobranchia: Acochliidae)
from Fiji

by

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Abstract. A new species of freshwater opisthobranch, *Acochlidium fijiensis*, collected from stones in the Nasekawa River, Vanua Levu, Fiji, is described and its gross anatomical features are discussed and compared with those of other species of *Acochlidium*. Individual *Acochlidium fijiensis* reached maturity from July to October when the population was most abundant. Eggs were laid in a jelly mass attached to stones and the young hatched as veligers.

INTRODUCTION

The Acochliidae is the only opisthobranch order in which freshwater species are found and all of these have been discovered on islands. The freshwater species are *Strubellia paradoxa* (Strubell, 1892) from Guadalcanal, Solomon Islands, and Amboina, Indonesia (WAWRA, 1974), *Acochlidium amboinense* Strubell, 1892, from Amboina, *Acochlidium weberi* Bergh, 1896, from Flores (placed in the new genus, *Palliohedyle* by RANKIN [1979] but classification disputed by Wawra [personal communication]), *Acochlidium suteri* Wawra, 1979, from Sumba, Indonesia, *Acochlidium bay-erfehlmanni* Wawra, 1980, from Palau (WAWRA, 1980), and *Tantulum elegans* Rankin, 1979, from St. Vincent in the Caribbean (RANKIN, 1979).

MATERIALS AND METHODS

Acochlidium fijiensis was first collected 7 km upstream from the mouth of the Nasekawa River at the bridge on the Labasa-Savusavu highway on the island of Vanua Levu, the second largest island in Fiji (site, 16°40'S, 179°16'E) in October 1983 (HAYNES, 1988). Subsequently other Fijian streams and rivers have been searched for this species. The only other place where it has been found is 4 km upstream from the mouth of the Lami River, Viti Levu, the main island of Fiji (site, 18°06'S, 178°24'E). Bernadette Holthuis found 5 specimens of *A. fijiensis* in the Lami River in November–December 1988. Small *A. fijiensis* populations may exist elsewhere in Vanua Levu and Viti Levu but, because individuals are well camouflaged and blend with the stones under which they live, they are difficult to detect.

Radulae were dissected from three preserved *Acochlidium fijiensis*. They were cleared with 10% potassium hydroxide and mounted in glycerine. The penis glands were removed from each dissected specimen, mounted in glycerine, and examined under a stereoscopic microscope.

For histology, specimens were killed and fixed in Bouin's fluid. Best results were obtained when the animals were first relaxed by lowering their temperature to about 4°C in the refrigerator. Extended, torpid specimens were immersed in ice-cold Bouin's fluid for 1 hr followed by 24 hr at room temperature. Fixed specimens were washed in running tap water for 12 hr, dehydrated in a graded series of ethanol dilutions (10–100%), cleared in xylene, and embedded in paraffin wax (melting point 60°C) under vacuum. Sections were cut at 7 µm and stained with Erlich's haematoxylin and eosin.

Water samples were analyzed by the Institute of Natural Resources, University of the South Pacific. In general, methods for chemical analysis of water samples were those described in *Standard Methods for the Examination of Water and Wastewater* (AMERICAN PUBLIC HEALTH ASSOCIATION, 1981).

TAXONOMY

Acochlidium fijiensis Haynes & Kenchington,
sp. nov.

(Figures 1–6)

Type locality: Nasekawa River, Vanua Levu, Fiji. Collection site at 16°40'S, 179°16'E.

Type specimens: The holotype (LACM 2457) and 2 paratypes (LACM 2458) have been deposited in the Los

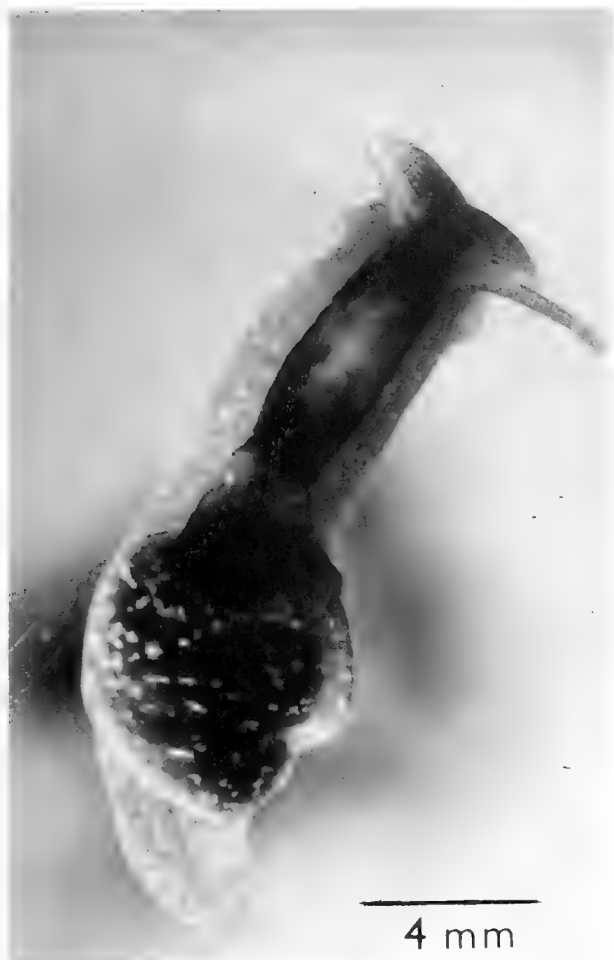


Figure 1

Photograph of a live *Acochlidium fijiensis*. The irregular pattern of white patches over the hump and foot is caused by spicules.

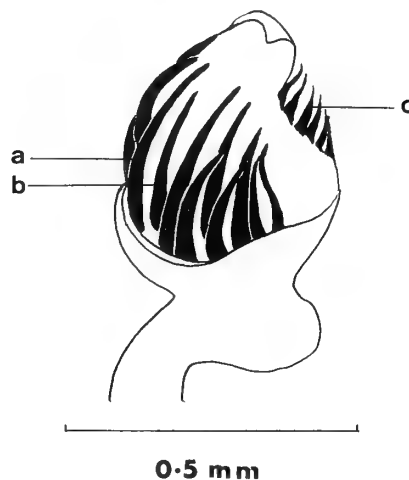


Figure 3

Penis gland of *Acochlidium fijiensis* showing: a, outer row of hooks; b, inner row of hooks; c, 6 small spines on the edge of the vas deferens opening.

Angeles County Museum of Natural History. Ten paratype specimens of *Acochlidium fijiensis* have been deposited in the Naturhistorisches Museum Wien, Inventory Number 84.901, and 7 paratypes, a radula, a penis permanently mounted in glycerine and slides of sectioned gonads are held in the Biology Department, School of Pure and Applied Sciences, University of the South Pacific, Suva. The dissected specimens were collected in January 1988; holotype, paratypes, and sectioned specimens were collected in July 1989. All type specimens were collected by A. Haynes.

Size, abundance and maturity: Table 1 indicates the relative abundance and size of specimens of *Acochlidium*

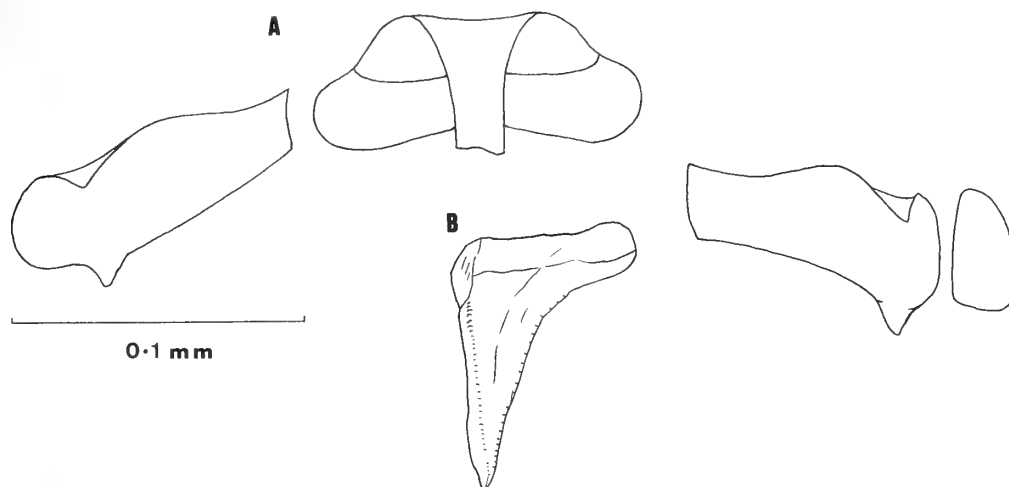


Fig. 2

Figure 2A. Ventral view of a row of radula teeth of *Acochlidium fijiensis*. B. Side view of median tooth showing fine serrations.

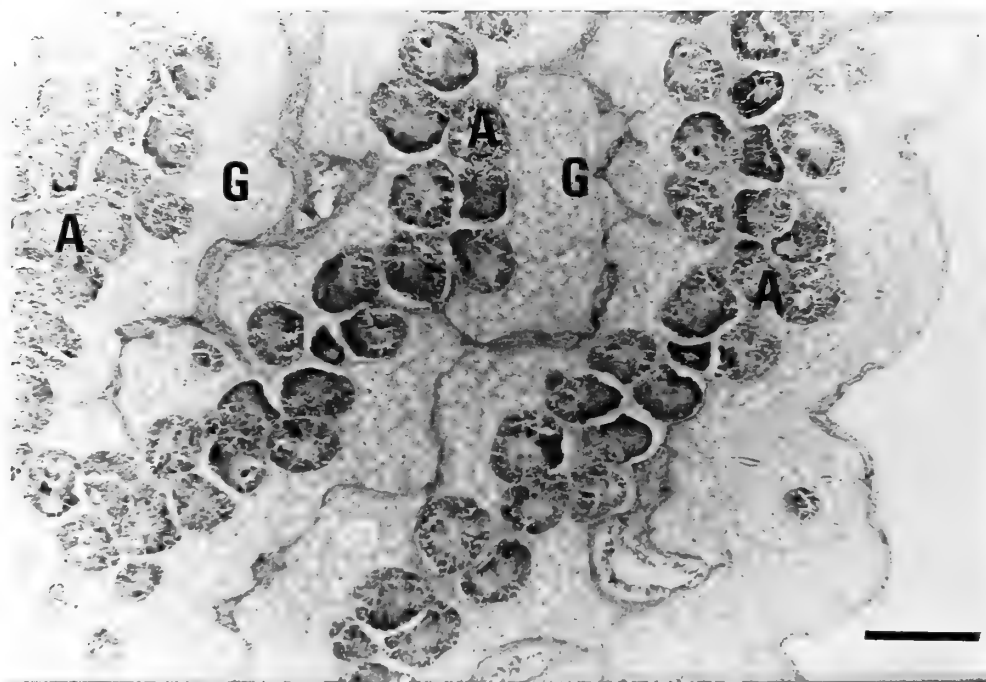


Figure 4

Coronal (horizontal longitudinal) section of the visceral hump of *Acochlidium fijiensis* stained with haematoxylin and eosin showing the extensive distribution of ovotestis acini (A) embedded in diverticula of the digestive gland (G). Scale bar = 0.1 mm.

fijiensis collected from the Nasekawa River on five occasions from October 1983 to July 1989. *Acochlidium fijiensis* was most abundant in October 1983 and July 1989, and individuals were also largest in July 1989 when their body hump was enlarged because they were reproductively mature. Histological sections of *A. fijiensis* specimens collected from the Nasekawa River in January 1988 and from the Lami River in November–December 1988 showed undeveloped gonadal tissue. Sections of specimens collected in July 1989 contained mature gonads (Figures 4, 5). This suggests that *A. fijiensis* has a well-defined breeding season (July–August, or perhaps longer during the cool, dry season) and that, after breeding, either the gonads disintegrate or each individual breeds only once in its lifetime. In the mature individuals that had been prepared for histology, abundant yolk granules and sperm were noted, but very few oocytes could be seen. Presumably these specimens had already spawned.

Habitat: Specimens of *Acochlidium fijiensis* were found on the underside of stones and rocks in shallow water, 60–140 mm deep, near the water's edge in both the Nasekawa

and Lami rivers. When *A. fijiensis* were kept in the laboratory, they always moved to the underside of the stones.

At the site in the Nasekawa River, the water level rose as much as 400 mm at high tide when heavy rain had been falling. However, when this occurred, there was little difference in the conductivity (or total ions) of the water at high and low tides (Table 2); therefore, the rise in water level is due to a back up of river water and not to inflowing seawater.

The chemical content of the water was similar at each sampling time and at high and low tides (Table 2). The water temperature was 29°C in October 1983 when *Acochlidium fijiensis* was abundant but at other times when the site was visited the temperature was 25–26°C (Table 2).

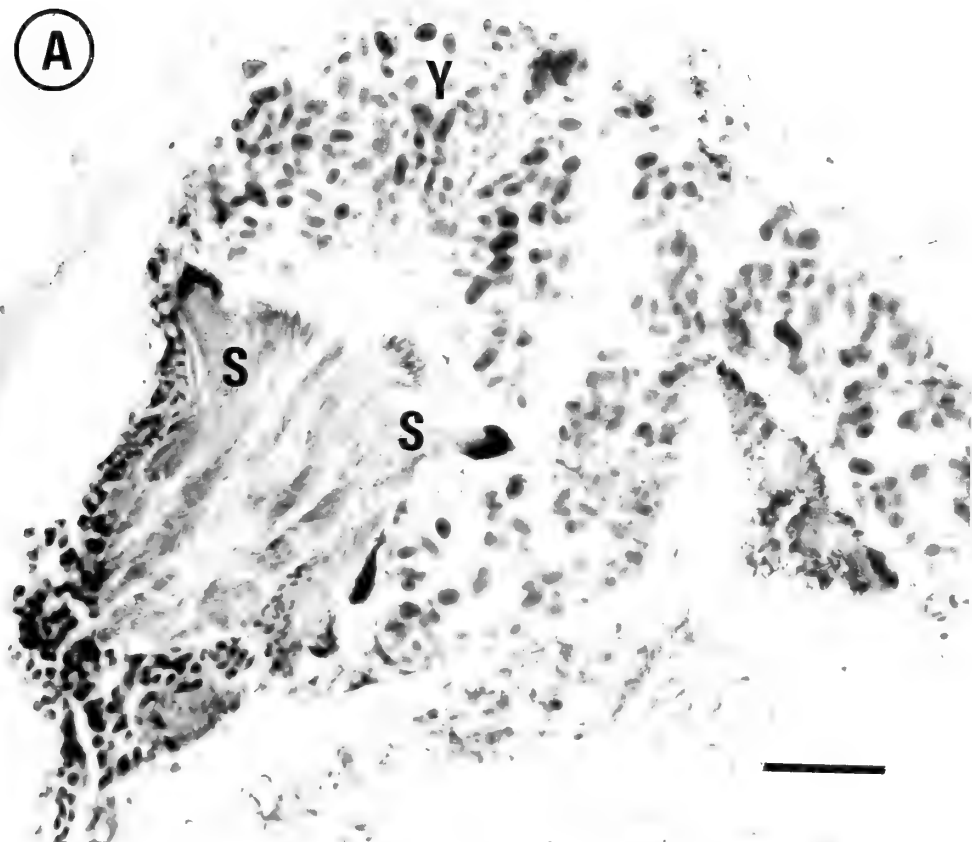
General Description

Diagnosis: Length of animal up to 19 mm, foot longer than visceral hump, which is rounded at the posterior (except when eggs have been shed, when the posterior may be ragged and pointed). Color cream-yellow, with wide

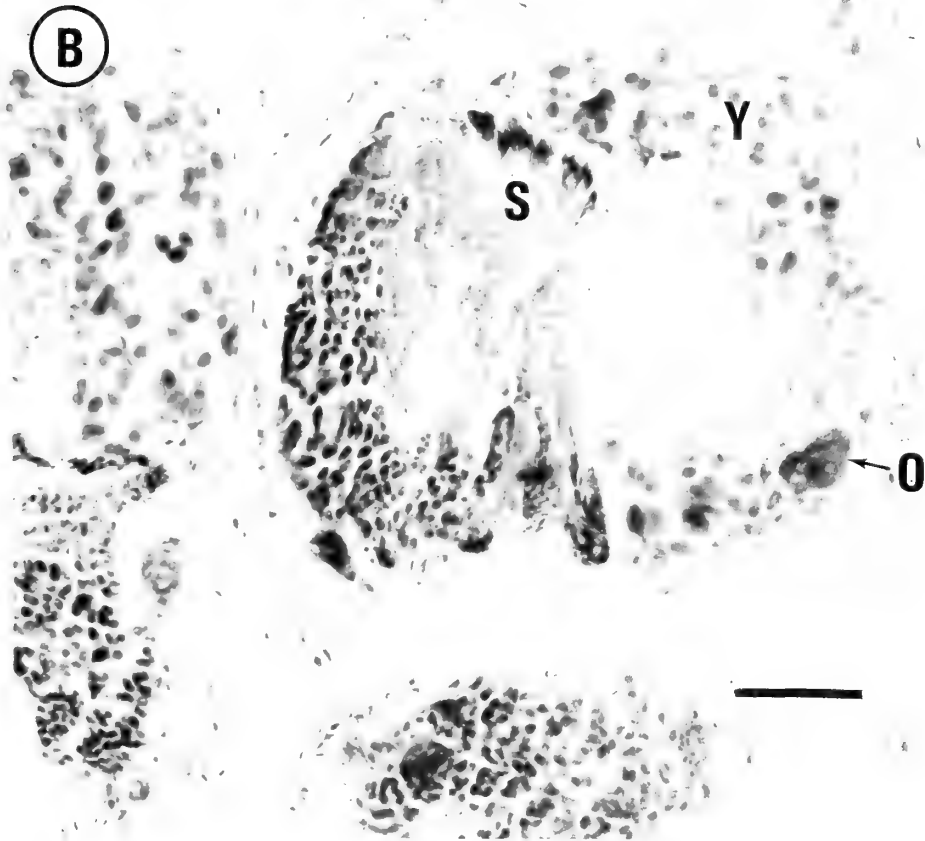
Figure 5

Histological sections through the ovotestis of *Acochlidium fijiensis* stained with haematoxylin and eosin. A. See abundant spermatozoa (S) and yolk granules (Y). B. See spermatozoa, yolk granules and a possible oocyte (O). Scale bar = 50 μ m.

(A)



(B)



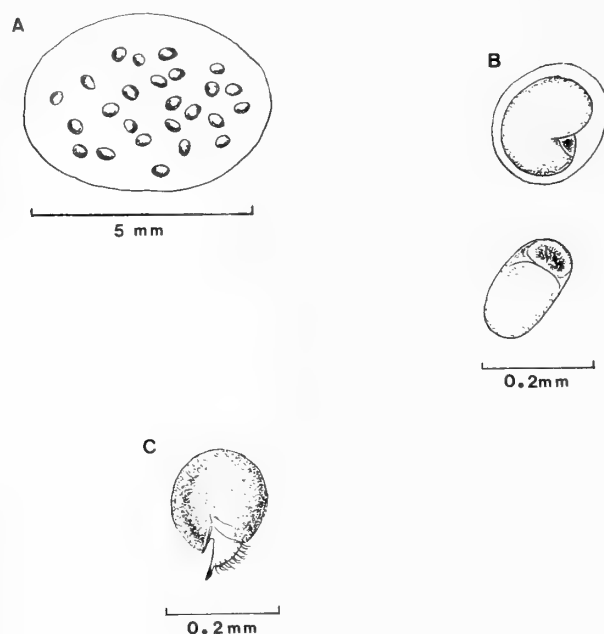


Figure 6

Acochlidium fijiensis. A. Developing eggs embedded in a jelly mass. B. Developing veligers, one still inside the egg membrane. C. Veliger larva swimming, after escaping from the egg membrane.

brown stripes across the dorsal side. Rhinophores (3.5 mm live; 1.8 mm preserved) longer than the anterior pair of tentacles (1.6 mm live; 0.8 mm preserved). Spicules present on visceral hump and foot (Figure 1).

Radula: Asymmetrical with formula $50 \times (1 \cdot 1 \cdot 2 \cdot)$. Left marginal plate lacking and rachidian (median) tooth finely serrated (Figure 2A, B).

Hermaphrodite: The penial armature consisting of a double row of long, curved hooks that form a border that almost surrounds the penial gland. A line of 6 small spines borders one side of the vas deferens opening (Figure 3).

Reproduction and development: *Acochlidium fijiensis* is a hermaphrodite. This conclusion is based on an observed spawning followed by dissection revealing a well-devel-

Table 1

The abundance and size of *Acochlidium fijiensis* collected from the Nasekawa River at different times.

Date	Number found	Duration of collection (hr)	Size (mm)
22 October 1983	16	1	not measured
7 August 1984	1	0.5	15
18–19 October 1985	12	6	6–11
19–20 January 1988	20	6	2–12
17 July 1989	30	2	10–19

Table 2

Physical and chemical parameters at the collecting site of *Acochlidium fijiensis* in the Nasekawa River.

	22 October 1985		22 January 1988	
	Low tide	High tide	Low tide	High tide
Temperature (°C)	26	25	25	25
Water depth (mm)	60–140	460–600	60–140	60–160
Water speed (cm·s ⁻¹)	0–30	0–10	0–30	0–30
pH	6.8	6.7	7.4	7.4
Conductivity (μs·cm ⁻¹)	97.9	100.7	102.6	102.6
Total nitrogen (mg·L ⁻¹)	8.2	7.1	2.5	2.5
Total phosphorus (μg L ⁻¹)	62.0	74.0	21.3	21.3
Ca (mg L ⁻¹)	7.8	8.2	9.2	9.2
Mg (mg L ⁻¹)	5.5	5.6	4.1	4.1
Na (mg L ⁻¹)	4.4	4.8	6.6	6.6
K (mg L ⁻¹)	0.26	0.29	0.85	0.85

oped penis. Also, sections of gonads (Figures 4, 5) show typical ovotestis composed of numerous acini, which are extensively distributed throughout the visceral hump where they are embedded amongst the diverticula of the digestive gland. In the specimens examined, acini were dominated by spermatozoa, spermatids, and associated generative tissue. Although yolk material was abundant, few oocytes were seen.

The spawning occurred in a 15-mm-long specimen that had been collected on 7 August 1984 and transferred to an aquarium. Thirteen days after capture it laid eggs, and three days later it died. The jelly mass was attached to two separate stones: one mass contained 31 eggs and the other 25 eggs (Figure 6A). The yellow eggs were embedded in clear jelly. After 10 days veligers were observed moving within the jelly (Figure 6B). After a further 12 days some of the veligers had escaped from the jelly mass and were swimming freely (Figure 6C). No veligers survived more than two days after leaving the jelly mass.

Discussion

A comparison of live *Acochlidium fijiensis* with other live *Acochlidium* species is not possible as no descriptions of the latter are available. Preserved specimens of *A. fijiensis* were similar in appearance to those described by Wawra for *A. sutteri* and *A. bayerfehlmanni*. The radula of *A. fijiensis* was asymmetrical, as were those of *A. sutteri* (WAWRA, 1979) and *A. bayerfehlmanni* (WAWRA, 1980). In the case of *A. fijiensis*, the number of rows of teeth was 50 compared with 52–56 for other *Acochlidium* spp. except *A. weberi*, which had 93–103 (WAWRA, 1979). The rachidian teeth appeared to be comparatively narrower (110 μm compared with 200 μm in *A. amboinense* and *A. sutteri* and 210–230 μm in *A. bayerfehlmanni*) and stouter, al-

though the laterals were approximately the same length (110–150 μm) (WAWRA, 1979, 1980) (Figure 2).

The male genital system of *Acochlidium fijiensis* was also similar to that of *A. sutteri* and *A. bayerfehlmanni*, with the male opening at the base of the right rhinophore (WAWRA, 1979, 1980). The armature on the penial gland appeared to be more similar to that of *A. bayerfehlmanni* than *A. sutteri*. However, the hooks in a double row nearly surrounding the penial gland in *A. fijiensis* were long and curved and the 6 small sharp spines were in a row on one side of the penis opening (Figure 3). In *A. bayerfehlmanni* the hooks are smaller and straighter and are not so extensive.

The general anatomy of *Acochlidium fijiensis* more closely resembled that of *A. bayerfehlmanni* than *A. sutteri* but the penial armature was distinctly different from both. Live *A. fijiensis* were smaller (19 mm long) than *A. bayerfehlmanni* (25 mm long) (WAWRA, 1980). However, because such characteristics as the presence or absence of spicules and the comparative length of rhinophores and anterior tentacles have not previously been recorded, it is impossible to use them for comparisons within the genus *Acochlidium*.

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Taxonomy of Japanese Species of the Genera *Mopalia* and *Plaxiphora* (Polyplacophora: Mopaliidae)

by

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Abstract. Four species of the chiton genus *Mopalia* and one species of the genus *Plaxiphora* are recognized in the intertidal and sublittoral zones of Japan: *M. middendorffii* (Schrenck, 1861), *M. retifera* Thiele, 1909, *M. schrenckii* Thiele, 1909, *M. seta* Yakovleva, 1952, and *Plaxiphora integra* (Is. Taki, 1954). *Mopalia hirsuta* Is. Taki, 1938, is a synonym of *M. middendorffii*. The Japanese records of *M. wosnessenskii* (Middendorff, 1847a) may be attributable to misidentification; therefore, no West Pacific species of the genus *Mopalia* is confirmed to occur in common with the East Pacific. The transfer of *Mopalia integra* into *Plaxiphora* is affirmed. *Plaxiphora integra* is newly recorded from the Ogasawara Islands as a southern extension of distribution. The shells, girdle elements, radula, and digestive tract of each species are described and illustrated.

INTRODUCTION

The genus *Mopalia* is endemic to the North Pacific. Eighteen species occur along the west coast of North America (LYONS, 1988), and several species are known from the northwestern Pacific. In Japan and adjacent waters, Is. TAKI (1962) and Iw. TAKI (1964) listed seven species: "*Mopalia* (*Mopalia*) *wosnessenskii* (Middendorff, 1847), *M. (M.) middendorffii* (Schrenck, 1867), *M. (M.) retifera* Thiele, 1909, *M. (M.) schrenckii* Thiele, 1909, *M. (M.) hirsuta* Is. Taki, 1938, *M. (M.) seta* Yakovleva, 1952, and *M. (Hachijomopalia) integra* Is. Taki, 1954." The descriptions on specimens from the Japanese coast were confined to only three species, *M. retifera*, *M. hirsuta*, and *M. integra*. The present paper describes the morphological characters of each species and reports on their distribution along the Japanese coast. The systematic position of *Mopalia* (*Hachijomopalia*) *integra*, which was previously transferred by KAAS & VAN BELLE (1980) from *Mopalia* into *Plaxiphora*, is confirmed by examination of the new material collected from both the Hachijo and Ogasawara islands.

Family MOPALIIDAE Dall, 1889

Genus *Mopalia* Gray, 1847a

Type species: *Chiton hindsii* (Sowerby MS) Reeve, 1847 (S.D. by GRAY, 1847b).

Mopalia schrenckii Thiele, 1909

(Figures 1-15, 74, 78)

Type locality: 4-5 miles (6-8 km) west of Schamow Inlet, Terpeniya Bay, southeast Sakhalin, 15-20 fathoms (27-36 m).

Mopalia schrenckii THIELE, 1909:30, pl. 4, figs. 4-10; Is. TAKI, 1955:203, fig. 3; KAAS & VAN BELLE, 1980:117 (name only); SIRENKO, 1985:356-357 (distribution).

Mopalia schrenckii: YAKOVLEVA, 1952:78, fig. 33, frontis. fig. 3, pl. 5, fig. 1; KLIMOVA & SIRENKO, 1976:79, fig. 185; SIRENKO, 1976:90-91 (distribution).

Mopalia (*Mopalia*) *schrenckii*: Is. TAKI, 1962:33 (name only); Iw. TAKI, 1964:410 (name only).

Material examined: See Table 1.

Description: Animal small to medium in size, attaining 30 mm in body length, oblong in outline (Figures 1, 74).

Valves: Head valve (Figure 2) semicircular, apex moderately elevated, anterior slope straight to slightly convex, posterior margin widely V-shaped; tegmental surface with eight radiating rows of tubercular ribs, arranged in correspondence with slits; posterior edge dentate by elongate tubercles; interspaces between ribs with obliquely intersecting fine riblets, and points of intersecting becoming granular; interior smooth and shiny; insertion plates long, squarish, nearly smooth; slits deep, usually eight in num-

ber, bounded on each side by conspicuous upturned edge of insertion plate; slit rays slightly grooved with minute slitlike pores.

Intermediate valves (Figure 3) wide, valve V widest, roughly rectangular in shape, but anterolateral corners obtusely angular, posterior margin nearly straight with slightly projected beak; dorsal ridge elevated, subcarinate to fairly carinate; side slopes nearly straight; lateral areas not elevated but clearly separated from central area by diagonal rib similar to ribs of head valve, bordered by elongate tubercles; central area with slightly inwardly curving longitudinal riblets, finer and sometimes anastomosing at jugal area, many threads between riblets; sculpture of lateral areas similar to that of interspace between ribs of head valve; interior smooth with low callus anterior to slightly grooved slit rays; sutural laminae wide with roundish anterior edge, separated by fairly wide sinus; insertion plates short, slightly projecting laterally beyond narrow eaves; sutural laminae and insertion plates with upturned edge at both sides of slit; one slit per side.

Tail valve (Figure 4) small, depressed, roughly trapezoid in shape, anterior margin gently convex, posterior end with shallow sinus; mucro slightly raised, situated near posterior end; anterior slope nearly straight; central area sculptured like that of intermediate valves; posterior area slightly raised, separated from central area by tubercular diagonal rib, then steeply descended posteriorly, with granular to nearly smooth surface; interior considerably roughened and thickened along posterior edge; sutural laminae broadly extended anteriorly, rounded at both corners, separated by V-shaped sinus; insertion plates short, obtuse at edge, roughened on lateral surface; one slit per side; slit rays inconspicuous, perceptible as series of minute pores.

Girdle: Girdle narrow, setose, slightly encroaching at sutures; perinotum covered by setae of various sizes and minute spicules; largest setae (Figure 7) situated on side of sutures and around terminal valves, others intermingle with smaller ones; each seta with many long threadlike bristles extending from dorsal groove; bristles flexible, gradually tapering toward distal end, tipped with minute spicule (Figure 7a) that is slender, hyaline, sharply pointed at tip, 20–25 μm in length and attached only at base; similar solitary bristles (Figure 6) dispersed or present in small tufts among densely set spicules, closely implanted on periphery; spicules on perinotum (Figure 8) minute, smooth, pointed at tip, brownish orange in color, 40–70 μm in length; marginal spicules (Figure 10) long, hyaline, obliquely striated, 110–135 μm in length; spicules on hyponotum (Figure 9) larger than those of perinotum, hyaline, striated along nearly entire length, 60–110 μm in length; spicules on pallial fold (Figure 11) slightly smaller, 45–70 μm in length and sparsely set.

Radula (Figures 12, 13, 78): Central tooth roughly rectangular with distal entire cutting edge, moderately swollen at middle, both sides of basal portion constricted and thick-

ened posteriorly, well concave at posterior surface, prop plate with rather pointed end; centro-lateral with small cusplike projection at outer lateral corner of dorsal edge, posterior portion strongly extended and reflexed laterally forming an auricular projection, propped by narrow basal plate extended laterally; major lateral with strong tridentate cusp sharply pointed at tip, middle denticle largest, outer lateral one smallest, shaft stout, thick, strongly keeled dorsally, dilated ventrally; inner small lateral solid, much elevated, narrowly extended anteriorly and dilated laterally at bottom; outer small lateral roughly rhomboid in shape, sinuated at both lateral surfaces, slightly extended anteriorly and posteriorly at bottom; major uncinus (Figure 13) slender, spoon-shaped, evenly arched posteriorly, slightly undulated twice laterally with rather short cusp; inner and middle marginals roughly rhomboid in shape, thick and platelike; outer marginal rather narrow, thin and platelike.

Digestive tract (Figure 5): Stomach pouchlike, but rather narrow, blind end situated at right side of visceral mass; anterior intestine originates from left side of stomach, dorsally runs posteriorly to right with U-shaped loop; intestinal valve recurves back and connects with posterior intestine; posterior intestine runs anteriorly within anterior intestine, descends between beginning of anterior intestine and intestinal valve, then turns to right and runs posteriorly, revolves one and a half times ventrally and leads back to long rectum.

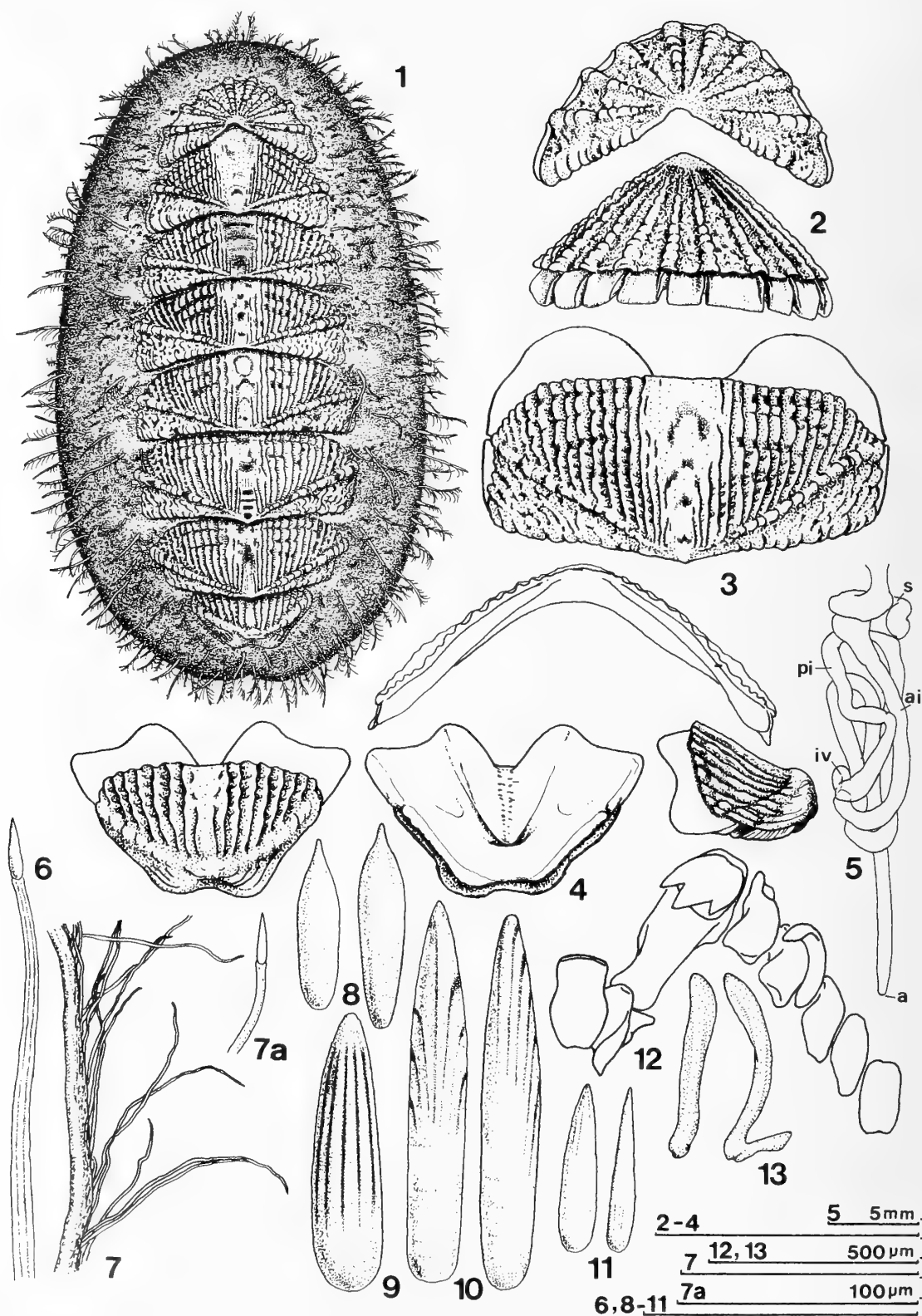
Gills, gonopore, and nephridiopore: Gills merobranchial and abanal, usually extending from under valve IV to under posterior margin of valve VII, with number of gills increasing with growth (Figure 14); gonopore typically located between posterior second and third gills, and nephridiopore situated one ctenidium behind the gonopore (between two posteriormost gills).

Heart: Heart with one pair of auriculo-ventricular ostia.

Coloration: Preserved valves varying from olivaceous green or dark yellow to orange, banded with white at around jugal area and maculated with brown; interior of valves white; perinotum uniformly brownish orange to light brown; hyponotum uniformly light brown.

Distribution: Hokkaido, southern Kuril Islands, Sakhalin, and the Sea of Japan coast of the USSR (Figure 15), on underside of stones in littoral and sublittoral zones. The deepest record is 50 m, off Shikotan Island (SIRENKO, 1976).

Remarks: This species can be sufficiently distinguished from the related species *Mopalia seta* Yakovleva, 1952, by its having shorter insertion plates, a shallow but distinct posterior sinus of the tail valve, finer bristles, and a smaller number of gills (Figure 14). The costate valve sculpture and threadlike bristles are reminiscent of *M. cirrata* Berry, 1919, but the latter species differs in its coarser sculpture,



Explanation of Figures 1 to 13

Figures 1-13. *Mopalia schrencki* Thiele, 1909. Figures 1-4: body length 19.5 mm, from Rausu. Figures 5, 7, 7a: body length 31.2 mm, from Saruru. Figures 6, 8-13: body length 23.4 mm, from Akkeshi.

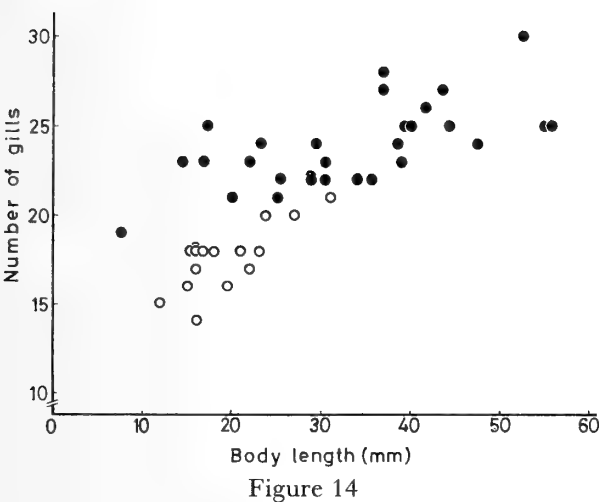


Figure 14
Relationship between body length and number of gills of two *Mopalia* species. Open circles, *M. schrencki* ($n = 16$); solid circles, *M. seta* ($n = 29$).
deep posterior sinus of the tail valve, and scalelike spicules of the perinotum.

Mopalia seta Yakovleva, 1952
(Figures 14, 16–30, 75, 80)

Type locality: Southern part of Japan Sea (by Yakovleva).

- Mopalia seta* YAKOVLEVA, 1952:77, fig. 32, frontis. fig. 7, pl. 4, fig. 3; SIRENKO, 1976:91 (distribution); SIRENKO, 1985: 356 (distribution); KAAS & VAN BELLE, 1980:118 (name only).
Mopalia wosnessenskii: Is. TAKI, 1955:204 (distribution) (*non* MIDDENDORFF, 1847a).
Mopalia (Mopalia) wosnessenskii: Is. TAKI, 1962:32 (name only); IW. TAKI, 1964:411 (name only); ISHIKAWA, 1966: 96 (in part) (all *non* MIDDENDORFF, 1847a).
Mopalia (Mopalia) seta: Is. TAKI, 1962:33 (name only); IW. TAKI, 1964:411 (name only).

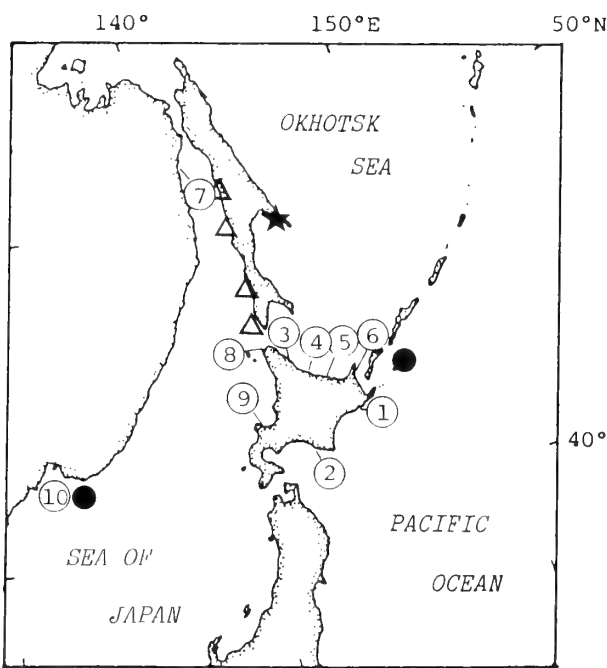


Figure 15
Distribution of *Mopalia schrencki*. Localities indicated as follows: numbers, this study (see Table 1); star, type locality; solid circles, SIRENKO (1976); triangles, SIRENKO (1985).

Material examined: See Table 2.

Description: Animal medium to large in size, attaining 55 mm in body length, elliptical in outline (Figures 16, 75).

Valves: Head valve (Figure 17) semicircular, apex fairly elevated, anterior slope straight to slightly convex; tegmental surface with eight radiating rows of tubercular ribs arranged in correspondence with slits; posterior edge dentate by smaller tubercles, but hardly raised; interspace

←

- Figure 1. Dorsal view of animal.
Figure 2. Head valve, dorsal and anterior views.
Figure 3. Valve IV, dorsal and anterior views.
Figure 4. Tail valve, dorsal, ventral, and lateral views.
Figure 5. Digestive tract, dorsal view.
Figure 6. Isolated bristle.
Figure 7. Seta, middle portion.
Figure 7a. Bristle of seta, distal end with spicule.
Figure 8. Spicules on perinotum.
Figure 9. Spicule on hyponotum.
Figure 10. Marginal spicules.
Figure 11. Spicules on pallial fold.
Figure 12. Radula, half row.
Figure 13. Major uncinus, posterior and lateral views.
Abbreviations: a, anus; ai, anterior intestine; iv, intestinal valve; pi, posterior intestine; s, stomach.

Table 1
Data of specimens of *Mopalia schrencki* used in this study.

Locality*	Collecting depth (m)	Number of individuals	Body length (mm)	Date collected	Collector
Pacific Coast					
1. Akkeshi	intertidal	3	21.3–23.8	10–13 July 1983	Y. Kuwahara
2. Higashi-shizunai	1	1	27.0	22 Aug. 1986	H. Saito
Okhotsk Sea					
3. Kitami-esashi	0.5–2	5	12.6–16.1	11 Aug. 1987	H. Saito
4. Saruru	1	1	31.2	18 Aug. 1986	H. Saito
Saruru	0.5	1	22.0	10 Aug. 1987	H. Saito
5. Saroma	8	1	ca. 23	5 June 1987	H. Hoshikawa
6. Rausu	5	2	18.0, ca. 20	29 July 1988	R. Inoue
Rausu	4	2	ca. 15, 19.5	—	I. Soyama
Japan Sea					
7. De Castries Bay	—	1	16.0	22 Aug. 1982	B. Sirenko
8. Wakkanai	unknown**	1	11.4	12 Aug. 1987	H. Saito
9. Oshoro	8–9	1	16.8	17 Aug. 1987	H. Saito
10. Vostok Bay	1–2	2	15.4, 21.0	1 Sep. 1980	B. Sirenko

* Locality number corresponds to that in Figure 15.

** Incidentally caught by gill net operated in depth probably shallower than 30 m.

between ribs with obliquely intersecting riblets; interior smooth, shiny; insertion plates well developed, long, squarish, nearly smooth; slits deep, usually eight in number, bounded on each side by conspicuous upturned edge of insertion plates; slit rays not grooved, appearing as whitish lines with series of minute slitlike pores.

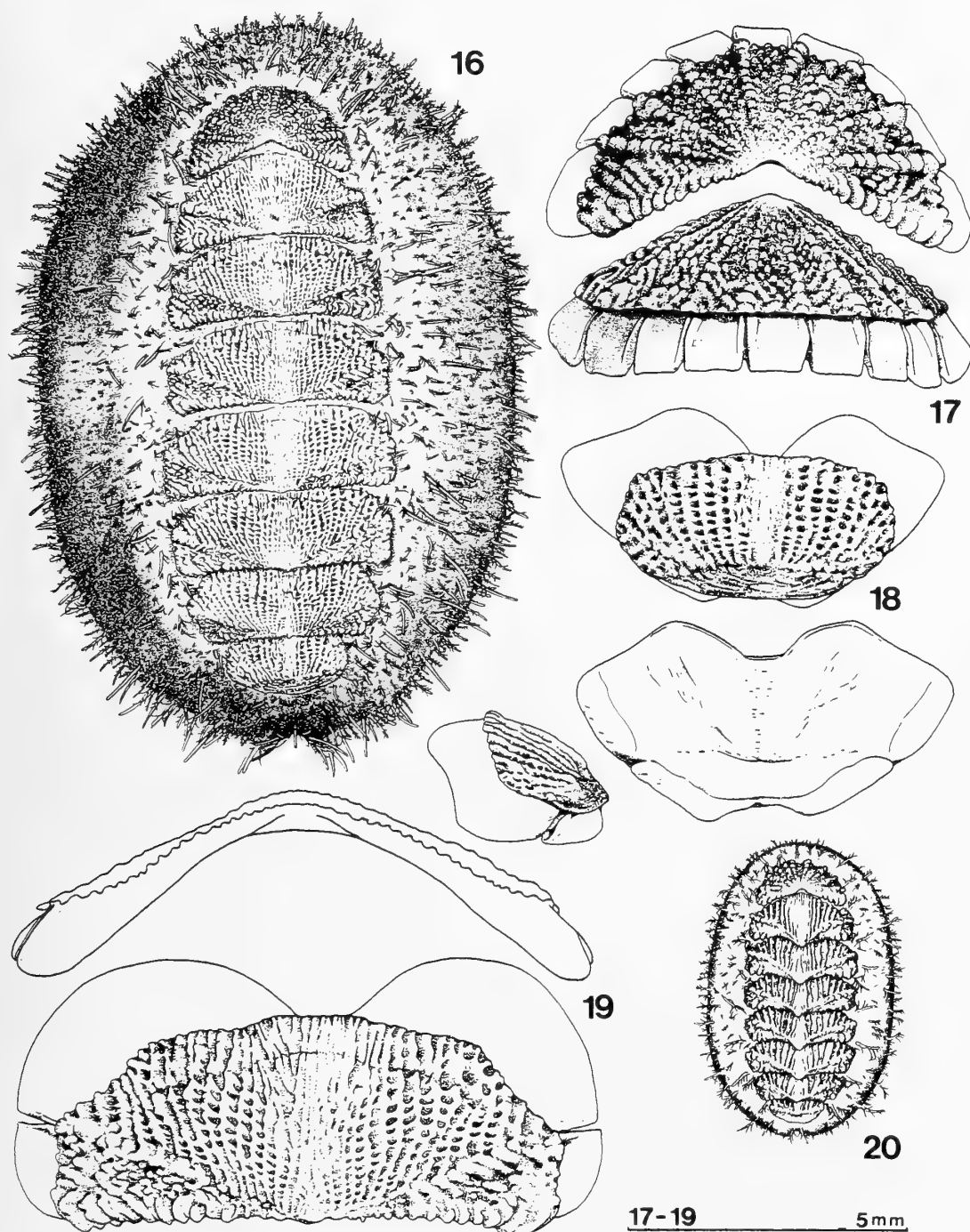
Intermediate valves (Figure 19) wide, valve V widest, anterior margin roughly rounded and posterior margin slightly concave, only slightly beaked, rather depressed and weakly carinate at dorsal ridge, with slightly convex side slopes; lateral areas not elevated but clearly separated from central area by diagonal rib similar to ribs of head valve, and posterior margin bordered by elongate tubercles; central area with longitudinal riblets, which are sometimes bifurcated near anterior margin, finer and coalescent at around jugal area, inner surface of these riblets buttressed by numerous, fine, clawlike, transverse riblets; sculpture of lateral areas similar to that between ribs of head valve, but riblets often arranged in herringbone or zigzag pattern; interior smooth, shiny with transverse callus extending from center to near slits; sutural laminae wide with roundish anterior edge, separated by widely V-shaped sinus; insertion plates long, strongly projecting laterally beyond narrow eaves; insertion plates and sutural laminae with upturned edge on both sides of slit; one slit per side; slit rays with series of minute pores and not grooved.

Tail valve (Figure 18) small, depressed, roughly oval in shape, rounded on both corners of anterior margin, hardly incised at posterior margin; mucro not raised and situated at about posterior third; anterior slope slightly convex, posterior slope behind mucro slightly concave; central area sculptured like that of intermediate valves; posterior area granular around mucro; interior thickened along

posterior edge; sutural laminae broadly extended anteriorly, anterior edge obliquely truncated, separated by widely V-shaped sinus; insertion plates short, obtuse at edge, roughened on lateral surface; one slit per side; slit rays with several minute slitlike pores and not grooved.

Girdle: Girdle wide, setose, moderately encroaching at sutures; perinotum densely covered by setae of various lengths and minute spicules; largest setae (Figure 21) situated on side of sutures and around terminal valves, others gradually becoming smaller toward periphery and intermingled with smaller ones on entire surface; each seta with many long, fine, curved bristles, thickest at middle, tapering toward both ends, tipped at distal end with minute spicules (Figure 21a) that are slender, hyaline, slightly curved, 30–70 μm in length, embedded in bristle in proximal half; similar bristles (Figure 22) dispersed as solitary ones or in small tufts among densely set spicules closely implanted on periphery; spicules on perinotum (Figure 24) minute, sharply pointed at tip, brownish orange in color, 55–70 μm in length; marginal spicules (Figure 25) long, hyaline, obliquely striated or nearly smooth, 145–185 μm in length; spicules on hyponotum (Figure 23) longer than those of perinotum, hyaline, striated, 95–125 μm in length; spicules on pallial fold (Figure 26) slightly more slender than other hyponotal spicules and sparsely set.

Radula (Figures 27, 28, 80): Central tooth roughly rectangular with distal cutting edge, slightly swollen at middle, constricted laterally and thickened posteriorly at bottom, concave on posterior surface, prop plate thick and rounded anteriorly; centro-lateral with small cusplike projection at outer lateral corner of dorsal edge, posterior portion strong-



Explanation of Figures 16 to 20

Figures 16–20. *Mopalía seta* Yakovleva, 1952. Figures 16–19. body length 29.0 mm, from Muroran. Figure 20. body length 7.6 mm, from Hamamasu.

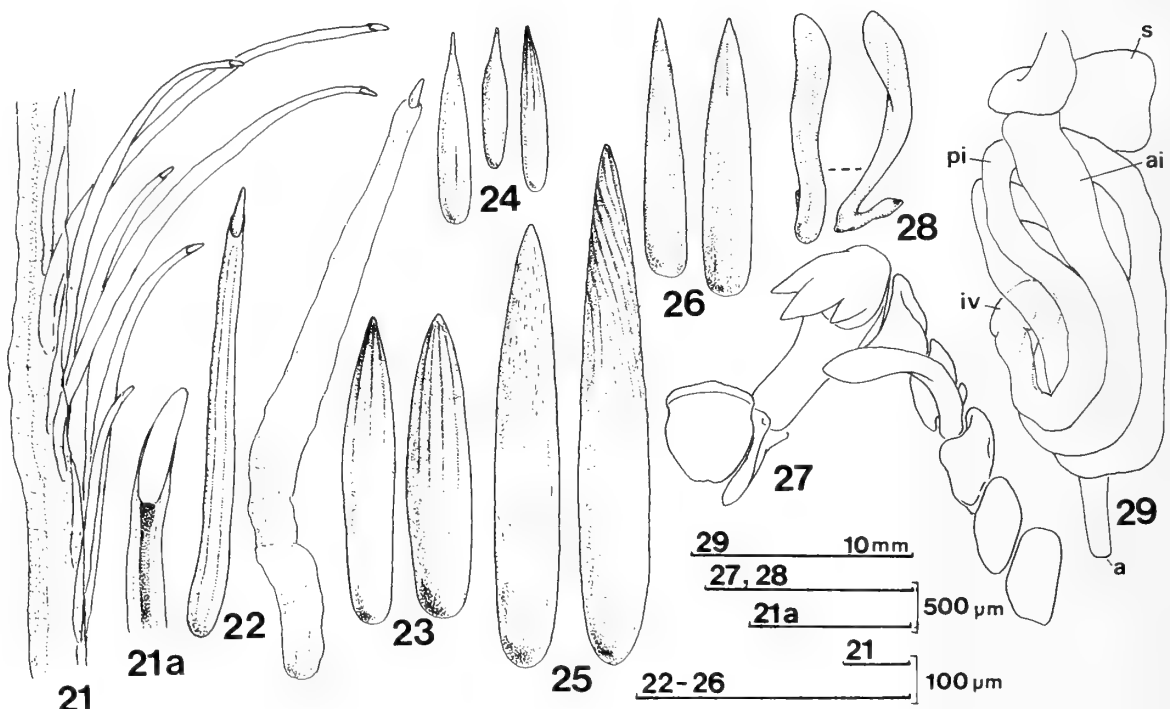
Figure 16. Dorsal view of grown animal.

Figure 17. Head valve, dorsal and anterior views.

Figure 18. Tail valve, dorsal, ventral, and lateral views.

Figure 19. Valve IV, anterior and dorsal views.

Figure 20. Dorsal view of young animal.



Explanation of Figures 21 to 29

Figures 21–29. *Mopalia seta* Yakovleva, 1952. Figure 21, 21a. body length ca. 22 mm, from Otamoi. Figures 22–26. body length 43.6 mm, from Muroran. Figures 27, 28. body length 29.0 mm, from Muroran. Figure 29. body length ca. 37 mm, from Hamamasu.

Figure 21. Seta, middle portion.

Figure 21a. Bristle of seta, distal end with spicule.

Figure 22. Isolated bristles.

Figure 23. Spicules on hyponotum.

Figure 24. Spicules on perinotum.

Figure 25. Marginal spicules.

Figure 26. Spicules on pallial fold.

Figure 27. Radula, half row.

Figure 28. Major uncinus, posterior and lateral views.

Figure 29. Digestive tract, dorsal view.

See Figure 1–13 for abbreviations.

ly extended and reflexed laterally forming auricular projection, propped by basal plate with obtuse end; major lateral with strong and tridentate cusp, denticles sharply pointed at tip, middle denticle longest, outer lateral one smallest; shaft stout, thick, strongly keeled dorsally, dilated ventrally but concave at middle of outer lateral side; inner small lateral solid, much elevated, extended anteriorly at bottom, deeply concave at outer lateral surface; outer small lateral elevated, roughly sigmoid in shape, sinuated at both lateral surfaces, slightly extended anteriorly and posteriorly at bottom; major uncinus (Figure 28) slender spoon-shaped, gently curved posteriorly but slightly angular at

middle; inner marginal thick, platelike, roughly rhomboid in shape, narrowing anteriorly and sinuated at inner side; middle marginal roughly rhomboid-shaped and outer marginal squarish, thin and platelike.

Digestive tract (Figure 29): Stomach pouchlike, blind end situated at right side of visceral mass; anterior intestine originates from left side of stomach, dorsally runs posteriorly to right with U-shaped loop; intestinal valve situated at middle of left side of intestinal mass, turns back and connects with posterior intestine; posterior intestine runs along inside of anterior intestine, turns to right, revolves

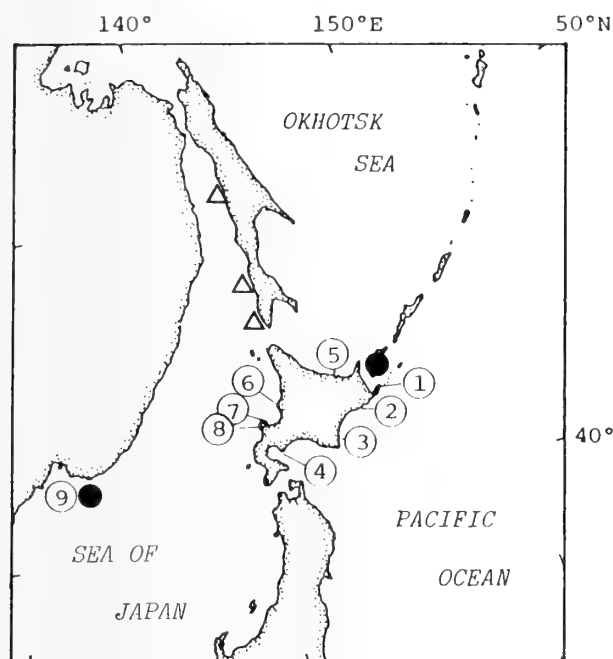


Figure 30

Distribution of *Mopalia seta*. Localities indicated as follows: numbers, this study (see Table 2); solid circles, SIRENKO (1976); triangles, SIRENKO (1985).

one and a half times ventrally, ascends and passes over intestinal valve, leads back to rectum.

Gill, gonopore, and nephridiopore: Gills merobranchial and abanal, usually extending from under posterior margin of valve III to that of valve VII, with number of gills gradually increasing with growth in adult stage (Figure 14); gonopore typically located between posterior second and third gills, and nephridiopore situated one ctenidium behind gonopore (between two posteriormost gills).

Heart: Heart with one pair of auriculo-ventricular ostia.

Coloration: Preserved valves olivaceous green maculated and banded with brown and blue-green; interior of valves white; perinotum uniformly light brown or yellowish brown; hyponotum light brown.

Distribution: Hokkaido, southern part of Kuril Islands, Sakhalin, and the Sea of Japan coast of the USSR (Figure 30), on rocks covered with sea weeds or on the underside of large stones in the littoral and sublittoral zones. The deepest record is 51 m, off Shikotan Island (KLIMOVA & SIRENKO, 1976).

Remarks: This species resembles *Mopalia ciliata* (Sowerby, 1840), *M. swanii* Carpenter, 1864, *M. schrencki* Thiele, 1909, *M. phorminx* Berry, 1919, and *M. spectabilis* G. I. McT. Cowan & I. McT. Cowan, 1977, in the possession of longitudinally costate sculpture of the valves. But, they are distinguishable from *M. seta* by the following points.

Table 2

Data of specimens of *Mopalia seta* used in this study.

Locality*	Collecting depth (m)	Number of individuals	Body length (mm)	Date collected	Collector
Pacific Coast					
1. Nosappu	intertidal	1	ca. 55	30 July 1988	S. Matsumura
Nosappu	intertidal	1	47.5	12 June 1987	S. Murakami
2. Akkeshi	intertidal	3	40.2-55.8	13 June 1987	S. Murakami
Akkeshi	intertidal	19	20.0-48.4	7-13 July 1983	Y. Kuwahara
Akkeshi	intertidal	3	34.0-38.5	18 Aug. 1982	H. Hoshikawa
Akkeshi	1	1	14.5	8 Aug. 1987	H. Saito
3. Hiroo	intertidal	1	44.3	10 Aug. 1984	Y. Kuwahara
4. Muroran	intertidal-1	11	16.9-43.6	16 Aug. 1987	H. Saito
Muroran	intertidal	3	29.5-35.5	10 Aug. 1983	Y. Kuwahara
Muroran	intertidal	1	17.0	25 May 1975	Y. Kuwahara
Okhotsk Sea					
5. Notoro	unknown**	1	ca. 20	24 July 1986	H. Hoshikawa
Japan Sea					
6. Hamamasu	0.5-3	3	7.6-ca. 37	17 Aug. 1986	H. Saito
7. Otamoi	2	1	ca. 22	16 Aug. 1986	H. Saito
8. Oshoro	intertidal-3	3	17.3-20.1	18 Aug. 1987	H. Saito
9. Vostok Bay	1-2	2	25.5, 35.6	1 Sep. 1980	B. Sirenko

* Locality number corresponds to that in Figure 30.

** Incidentally caught by trawl net for Yezo scallop.

(1) *M. ciliata*, *M. swanii* and *M. spectabilis* have a shorter tail valve with a wide posterior sinus and smoother sculpture of tegmentum. (2) *M. ciliata* has bristles with large and whitish spicules that are more similar to those of *M. retifera* than *M. seta*, the spicules attaining 300 μm in a specimen of body length 29 mm instead of 30–70 μm in almost the same sized specimen of *M. seta*. (3) *M. swanii* has sparse and short setae. (4) *M. spectabilis* has brilliant color, its red and turquoise-blue coloration of the valves is never present in *M. seta*, and it has longer spicules of the bristles, the spicules attaining 150 μm in a specimen of body length 34 mm. (5) *M. schrencki* has shorter insertion plates and finer bristles of the setae with smaller distal spicules and fewer gills (Figure 14). (6) *M. phorminx* has a secondary series of granules between the primary series on the head valve and between the diagonal rib and posterior margin of the intermediate valves, and shorter insertion plates.

The tegmental sculpture changes with growth. The sculpture of the central area is chiefly simple longitudinal riblets in an individual of 7.6 mm valve length (Figure 20). In older animals the sculpture becomes reticulate and the longitudinal riblets near the anterior margin are often bifurcated.

Earlier Japanese authors (e.g., IS. TAKI, 1962; IW. TAKI, 1964; ISHIKAWA, 1966) listed *Mopalia wosnessenskii* (Middendorff, 1847a) as a member of the Japanese mopaliid fauna, but no detailed description based on specimens from Japan has been given by anyone. *Mopalia wosnessenskii* has costate sculpture of the tegmentum, a shorter tail valve with a wide posterior sinus, and a wide girdle with numerous setae, which are clearly shown in the illustration by MIDDENDORFF (1847b). These features recall those of *M. ciliata*, so that the taxonomic status of *M. wosnessenskii* is confusing. DALL (1879) regarded it as a distinct species, but later (1921), as a subspecies of *M. ciliata*. ABBOTT (1974) and KAAS & VAN BELLE (1980) also regarded it as a subspecies of *M. ciliata*, while PILSBRY (1893) and LELOUP (1942) treated it as a variety of *M. ciliata*. In spite of considerable effort to confirm the occurrence of *M. wosnessenskii* or *M. ciliata* in Japanese waters, no specimen referable to this species has been found either on shore or in any museum or private collections, though *M. retifera*, *M. schrencki* and *M. seta* were commonly found. Judging from the similarity in general appearance between *M. seta* and the *M. ciliata-wosnessenskii* complex, the Japanese records of the latter taxon may be attributable to a misidentification. Therefore, none of the West Pacific species of the genus *Mopalia* is confirmed to occur in common with those of the East Pacific.

Mopalia middendorffii (Schrenck, 1861)

(Figures 31–45, 73, 81)

Type locality: De Castries Bay, Sea of Japan coast of the USSR.

Chiton middendorffii SCHRENCK, 1861:89; SCHRENCK, 1862 (1861):408; SCHRENCK, 1867:278–281, pl. 12, figs. 1–8.
Mopalia middendorffii: PILSBRY, 1893:301, pl. 62, figs. 88–92; THIELE, 1909:30, pl. 3, figs. 53–60; SIRENKO, 1976: 91 (distribution); SIRENKO, 1985:357 (distribution); YAKOVLEVA, 1952:76–77, fig. 31, frontis. fig. 8, pl. 4, fig. 2.
Mopalia hirsuta IS. TAKI, 1938:347–350, pl. 14, fig. 11, pl. 21, figs. 2, 4–6, pl. 23, figs. 12, 13; IS. TAKI, 1955:203, fig. 2; KAAS & VAN BELLE, 1980:60 (name only).
Mopalia middendorffii: IS. TAKI, 1955:203, fig. 1; KAAS & VAN BELLE, 1980:85 (name only).
Mopalia (Mopalia) hirsuta: IS. TAKI, 1962:33 (name only); IW. TAKI, 1964:410 (name only); ISHIKAWA, 1966:96 (distribution, as *hirsuta*).
Mopalia (Mopalia) middendorffii: IS. TAKI, 1962:33 (name only); IW. TAKI, 1964:411 (name only).

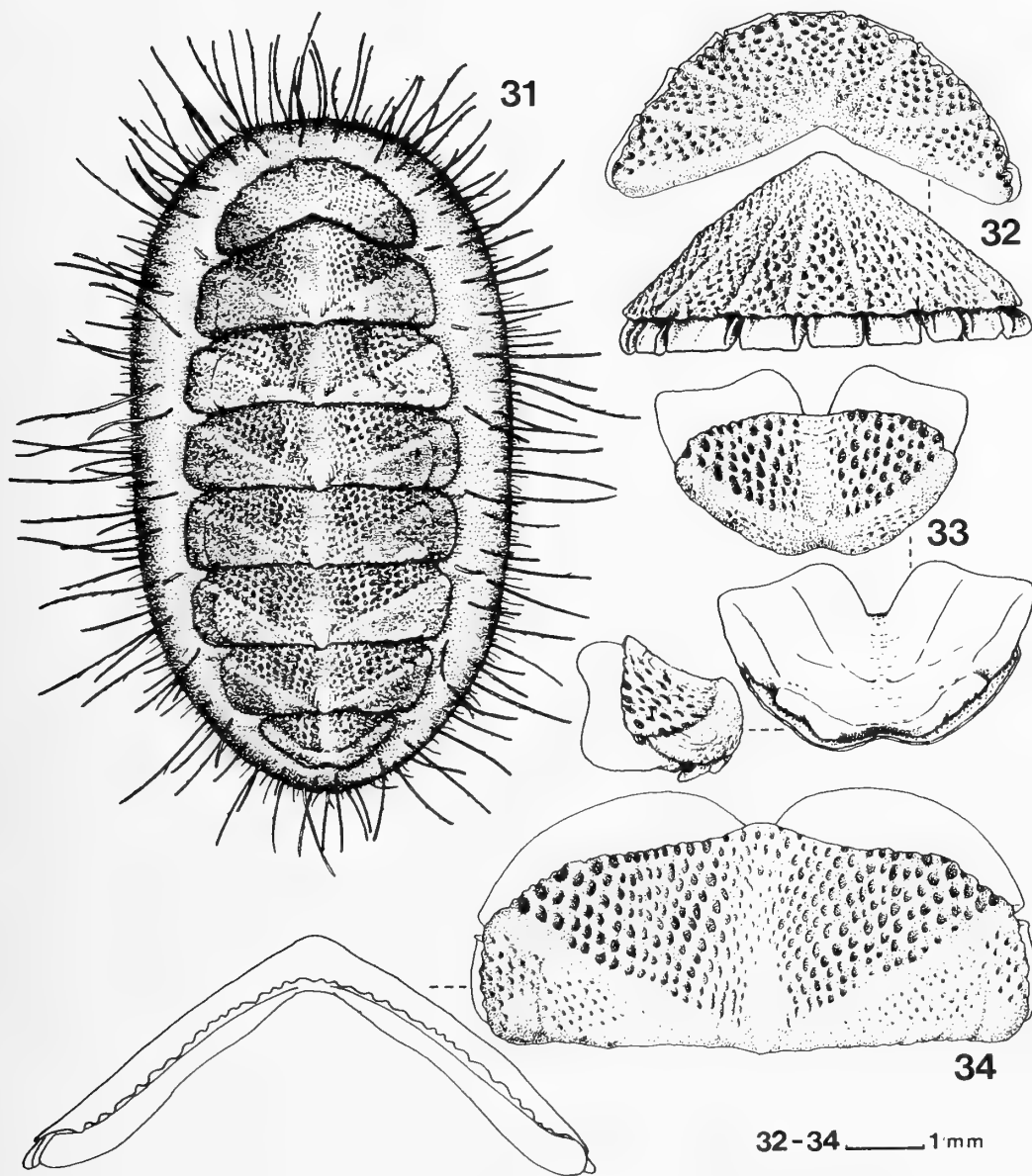
Material examined: See Table 3.

Description: Animal small to medium in size, attaining 30 mm in body length, oblong in outline (Figures 31, 73).

Valves: Head valve (Figure 32) thin, semicircular with moderately peaked apex, anterior slope nearly straight; tegmental surface with eight nearly smooth radiating ribs that correspond with slits, interspace between ribs finely pitted, appearing finely reticulate; posterior margin nearly smooth, slightly raised; interior smooth, shiny without callos, bordered by folded tegmentum that is conspicuous and triangular at top; insertion plates long, squarish, nearly smooth; slits deep, usually eight in number and bounded on each side by conspicuous tile-like upturned edge of insertion plates; slit rays appear as white lines with series of minute slitlike pores and not grooved.

Intermediate valves (Figure 34) wide, valve V widest, rectangular in shape, anterior margin gently convex, posterior margin almost straight, slightly beaked and smooth, much elevated and subcarinate at dorsal ridge with nearly straight side slopes; lateral areas much elevated, diagonal ribs hardly separable; central area finely reticulate, appearing as pitted flat surface rather than granularly ribbed; meshes or pits of reticulum moderately deep, squarish, almost equal in size except in jugal area; lateral areas have reticulation similar to that of head valve, often obsolete; posterior margin nearly smooth; interior smooth with callos extending from midline to near slit; sutural laminae thin, wide, regularly arched at anterior edge, separated by widely V-shaped sinus; insertion plates thin, short but slightly projecting laterally beyond narrow and spongy eaves; insertion plates and sutural laminae with upturned edge on both sides of slits; one slit per side; slit rays appear as series of minute pores and not grooved.

Tail valve (Figure 33) small, roughly oval in shape, anterior margin gently convex, shallowly sinuated at posterior end; mucro raised, situated near posterior end; anterior slope slightly concave and posterior slope steeply descending to posterior sinus; central area sculptured like that of intermediate valves; posterior area raised and sculptured like that of lateral areas of intermediate valves; in-



Explanation of Figures 31 to 34

Figures 31–34. *Mopalia middendorffii* (Schrenck, 1861). Valve length 16.9 mm, from Oshoro.

Figure 31. Dorsal view of animal.

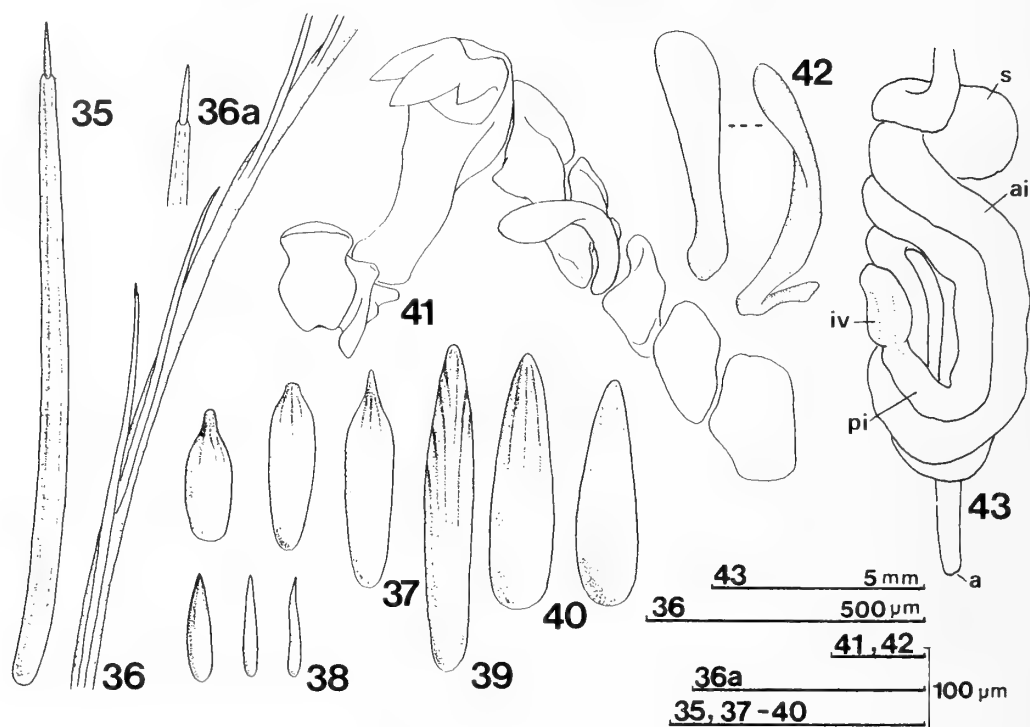
Figure 32. Head valve, dorsal and anterior views.

Figure 33. Tail valve, dorsal, ventral, and lateral views.

Figure 34. Valve IV, anterior and dorsal views.

terior thickened along posterior edge; sutural laminae broadly extended anteriorly, truncated but roundly projecting at inner corner of anterior edge, separated by V-shaped sinus; insertion plates short, obtuse at edge, considerably roughened on lateral surface; one slit per side; slit rays with several slitlike pores and not grooved.

Girdle: Girdle rather narrow, setose, slightly encroaching at sutures; perinotum covered by numerous setae of various lengths and minute spicules; largest setae (Figure 36) situated on side of sutures and around terminal valves, subsequent ones gradually becoming finer and shorter toward periphery; each seta with several rather short, fine, nearly



Explanation of Figures 35 to 43

Figures 35–43. *Mopalia middendorffii* (Schrenck, 1861). Valve length 16.9 mm, from Oshoro.

Figure 35. Isolated bristle.

Figure 36. Seta, middle portion.

Figure 36a. Bristle of seta, distal end with spicule.

Figure 37. Spicules on perinotum.

Figure 38. Spicules on pallial fold.

Figure 39. Marginal spicule.

Figure 40. Spicules on hyponotum.

Figure 41. Radula, half row.

Figure 42. Major uncinus, posterior and lateral views.

Figure 43. Digestive tract, dorsal view.

See Figures 1–13 for abbreviations.

straight bristles with minute slender distal spicule (Figure 36a), 15–25 μm in length; similar bristles (Figure 35) found singly, or in small tufts among densely set perinotal spicules, closely implanted on periphery; spicules on perinotum (Figure 37) minute, sharply pointed at tip, usually striated at distal third, brownish orange in color, 50–90 μm in length; marginal spicules (Figure 39) slender, hyaline, strongly and obliquely striated, 95–125 μm in length; spicules on hyponotum (Figure 40) somewhat larger than those of perinotum, finely striated or nearly smooth, light brown in color, 60–95 μm in length; spicules on pallial fold (Figure 38) minute, extremely slender, hyaline, 30–45 μm in length, ca. 4 μm in diameter, intermingled with spicules of ordinary size, 30–40 μm in length and 10–12 μm in diameter.

Radula (Figures 41, 42, 81): Central tooth broad with distal cutting edge, both sides strongly constricted near top, swollen at middle, constricted again and thickened posteriorly at bottom, concave on posterior surface, prop plate with moderately sharp end; centro-lateral with cusplike projection at outer lateral corner of dorsal edge, posterior portion strongly extended and reflexed laterally, propped by basal plate with obtuse end; major lateral with tridentate cusp, denticles of which are slender, sharply pointed at tip, with middle denticle longest and outer one smallest; shaft strongly keeled dorsally, dilated ventrally; inner small lateral solid, much elevated, extended anteriorly at bottom, deeply concave at outer lateral surface; outer small lateral elevated, roughly rhomboid-shaped, sinuated at both lateral surfaces, slightly extended anteriorly and posteriorly

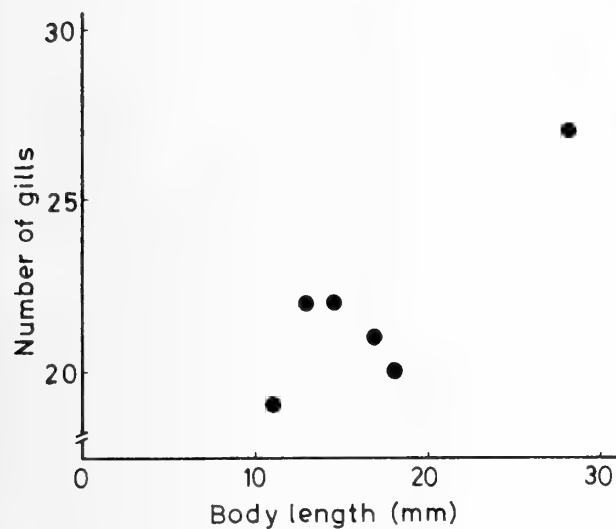


Figure 44

Relationship between body length and number of gills of *Mopalia middendorffii* (n = 6).

at bottom; major uncinus (Figure 42) slender, gently curved posteriorly with slender footlike basal plate directed anteriorly, shaft almost straight in posterior view; inner marginal thick, platelike, narrowing anteriorly and sinuated at inner lateral side; middle marginal roughly rhomboid-shaped; outer marginal thin, platelike and squarish in shape.

Digestive tract (Figure 43): Stomach pouchlike, blind end situated at right side of visceral mass, but not reaching dorsal surface; anterior intestine originates from left side of stomach, dorsally runs posteriorly with U-shaped loop; intestinal valve turns back and connects with posterior intestine; posterior intestine runs along inside of anterior intestine, descends between beginning of anterior intestine and intestinal valve, then turns to right, loops one and a half times ventrally and leads back to rectum.

Gills, gonopore, and nephridiopore: Gills merobranchial and abanal, usually extending from under middle or posterior end of valve III to that of valve VII, with number

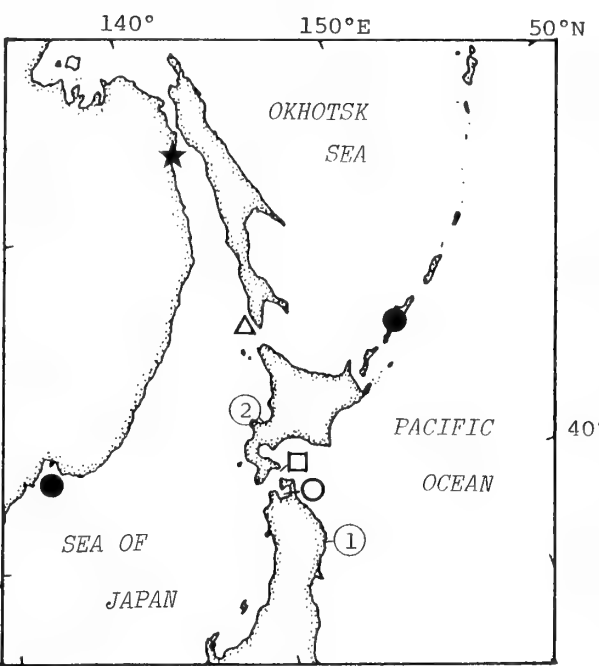


Figure 45

Distribution of *Mopalia middendorffii*. Localities indicated as follows: numbers, this study (see Table 3); star, type locality; solid circles, SIRENKO (1976); triangle, SIRENKO (1985); open circle, type locality of *Mopalia hirsuta* by Is. TAKI (1938); square, ISHIKAWA (1966).

increasing with growth (Figure 44); gonopore typically located between posterior second and third gills, and nephridiopore situated one ctenidium behind the gonopore (between two posteriormost gills).

Heart: Heart with one pair of auriculo-ventricular ostia.

Coloration: Preserved valves reddish brown with broad whitish areas along jugal area, or whitish with brownish bands on central area, jugal area pinkish; interior of valves translucent and color of tegmentum faintly visible, perinotum uniformly brownish orange; hyponotum same as perinotum except for whitish pallial fold.

Table 3

Data of specimens of *Mopalia middendorffii* used in this study.

Locality*	Collecting depth (m)	Number of individuals	Body length (mm)	Date collected	Collector
Pacific Coast					
1. Ozuchi	12	1	18.0	17 June 1983	H. Hoshikawa
Japan Sea					
2. Oshoro	6-10	5	11.0-28.1	17-19 Aug. 1987	H. Saito

* Locality number corresponds to that in Figure 45.

Distribution: Pacific coast of northern part of Honshu, northern part of Sea of Japan (Figure 45), on underside of stones in sublittoral zone. The shallowest recorded depth is 2 m in Vostok Bay (SIRENKO, 1976), and the deepest record is 60 m in Mutsu Bay (Is. TAKI, 1938, as *M. hirsuta*).

Remarks: Is. TAKI (1938) described *Mopalia hirsuta* based on a single small specimen (body length 9 mm) collected from Mutsu Bay. *Mopalia hirsuta* has elevated and subcarinated valves with reticulate sculpture, characteristic long setae with fine straight bristles, and brownish red coloration. These features agree well with those of *M. middendorffii*. Although he considered it to be closely related to *M. middendorffii*, Is. TAKI (1938) indicated the following morphological characters as sufficient to distinguish the two species: (1) coarse sculpture of the tegmen-tum, (2) denticulated posterior margin of the valves, (3) acute divergence of the intermediate valves, (4) small calcareous tip of bristles in the girdle, (5) minute strongly ridged scales on the perinotum, and (6) more elongate body.

The first two characters are juvenile features; both the sculpture and the posterior margin of the valves become smooth with growth. Characters (3), (5), and (6) reflect intraspecific variation. Taki measured a 105° divergence of the intermediate valves of the type specimen of *M. hirsuta* compared with 115° in the type of *M. middendorffii*, while the present specimens exhibit a range of 100° to 114°. The striations of the perinotal spicules were illustrated ambiguously by THIELE (1909) and those on the distal third of the spicules by YAKOVLEVA (1952). However, such striations or ridges were usually observed on the distal third of spicules in the material we examined; striations along the entire length of the spicules, as illustrated by Thiele and Taki, were also observed. Character (4) was described neither in the original description nor in any subsequent redescription of *M. middendorffii*. The fact that authors did not mention the spicules could be due to their being overlooked or because damaged specimens were being studied. Therefore, the above-mentioned characters are not significant to distinguish the species.

Mopalia retifera Thiele, 1909

(Figures 46–60, 76, 79)

Type locality: Not designated, but the following localities are given: Kagoshima; Hojo, Province Awa (Chiba Prefecture); Enoshima (Kanagawa Prefecture); Tsingtau; Gulf of Amur, east of Jankowsky Peninsula.

Mopalia retifera THIELE, 1909:30–31, pl. 3, figs. 61–64, pl. 4, figs. 1–3; Is. & IW. TAKI, 1929:148–153, figs. 32–43, pl. 2, fig. 2; LELOUP, 1942:57, fig. 26J; YAKOVLEVA, 1952:78–79, fig. 34, frontis. fig. 6, pl. 5, fig. 2; Is. TAKI, 1955:203, fig. 4; KLIMOVA & SIRENKO, 1976:79, fig. 184; SIRENKO, 1976:90 (distribution); KAAS & VAN BELLE, 1980:110 (name only).

Mopalia (Mopalia) retifera: Is. TAKI, 1962:33 (name only); IW. TAKI, 1964:410–411 (name only).

Mopalia (Mopalia) wosnessenskii: ISHIKAWA, 1966:96, pl. 1, fig. 9 (in part, non MIDDENDORFF, 1847a).

Material examined: See Table 4.

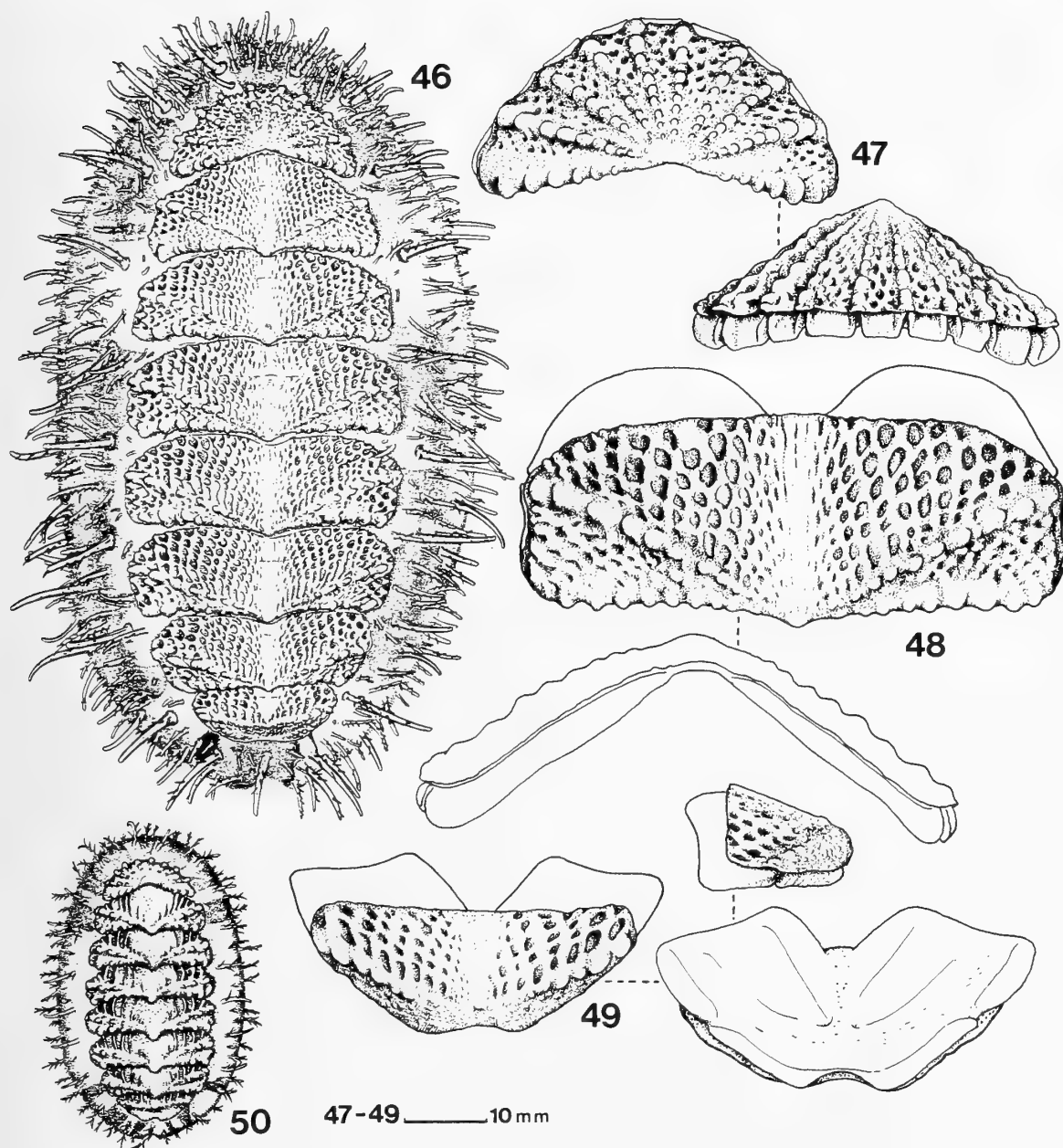
Description: Animal medium in size, attaining 40 mm in body length, oblong in outline (Figures 46, 76).

Valves: Head valve (Figure 47) semicircular, apex moderately elevated, anterior slope convex; tegmental surface with eight radiating rows of tubercular ribs, arranged in correspondence with slits; posterior edge dentate by somewhat elongate tubercles; surface between ribs with fine reticulation; interior smooth and shiny; insertion plates squarish with nearly smooth surface; slits distinct, usually eight in number, bounded on each side by conspicuous upturned edge of insertion plates; slit rays perceptible as series of minute slitlike pores.

Intermediate valves (Figure 48) rectangular, gently rounded at both corners of anterior margin, slightly beaked, moderately elevated and subcarinate at dorsal ridge, side slopes slightly convex; lateral areas only slightly elevated but clearly separated from central area by diagonal rib similar to tubercular ribs of head valve and bordered by dentate posterior margin; tegmental surface of central area regularly reticulate due to intersecting of inwardly arching longitudinal riblets and radial riblets originating from apex; mesh of reticulum squarish or rhomboid, fine and narrow at jugal area, gradually increasing in size toward margin; lateral areas with fine reticulation similar to surface between ribs of head valve but somewhat coarser; interior smooth with slight transverse thickening; sutural laminae wide, rather short, anterior margin slightly arcuate, separated by widely V-shaped sinus; insertion plates rather short, hardly projecting laterally beyond narrow spongy eaves; insertion plates and sutural laminae thickened and curved dorsally on sides of slit; slit rays not grooved, appearing as whitish lines with series of minute pores.

Tail valve (Figure 49) small, depressed, roughly triangular in outline, shallowly sinuated at posterior end; mucro hardly raised and situated near posterior third; anterior slope almost straight; central area sculptured like that of intermediate valves; posterior area granular; interior somewhat roughened, thickened along posterior edge; sutural laminae broad, anterior margin truncate or slightly concave, separated by V-shaped sinus; insertion plates short, obtuse at edge, posterior surface roughened; one slit per side; slit rays inconspicuous, perceptible as series of slitlike pores.

Girdle: Girdle rather narrow, setose, slightly encroaching at sutures; perinotum covered by setae of various sizes and minute spicules; setae on side of sutures and around terminal valves (Figure 51) larger than others; each seta with long, curved, hyaline spicules, smooth or finely striated, pointed at tip, up to 650 μ m in length; smaller setae closely set near anterior margin, sparsely set on rest of perinotum, intermingling with minute ones; spicules on perinotum (Figure 53) minute, slender, hyaline or brownish in color,



Explanation of Figures 46 to 50

Figures 46-50. *Mopalia retifera* Thiele, 1909. Figure 46. body length 17.2 mm, from Muroran. Figures 47-49. body length 16.5 mm, from Shimoda. Figure 50. body length 6.0 mm, from Oshoro.

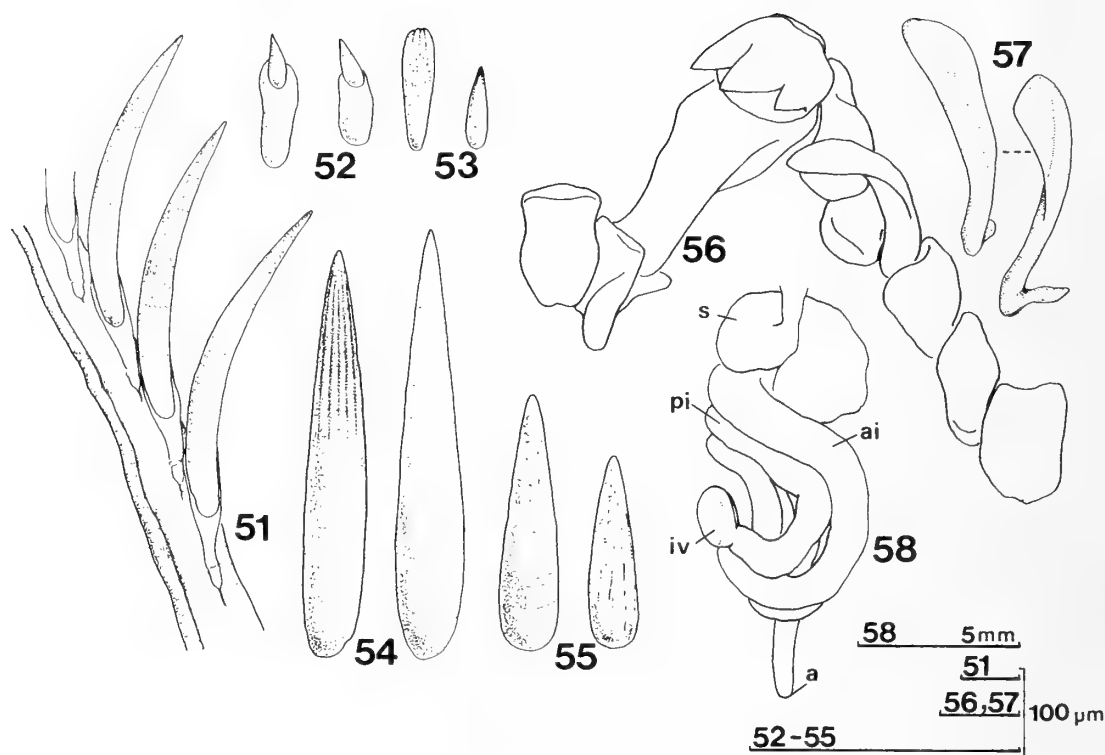
Figure 46. Dorsal view of animal.

Figure 47. Head valve, dorsal and anterior views.

Figure 48. Valve IV, dorsal and anterior views.

Figure 49. Tail valve, dorsal, ventral, and lateral views.

Figure 50. Dorsal view of young animal.



Explanation of Figures 51 to 58

Figures 51–58. *Mopalia retifera* Thiele, 1909. Figures 51–55. body length 17.2 mm, from Amakusa. Figures 56, 57. body length ca. 24 mm, from Miyato. Figure 58. body length 23.5 mm, from Muroran.

Figure 51. Seta, middle portion.

Figure 52. Isolated bristles.

Figure 53. Spicules on perinotum.

Figure 54. Marginal spicules.

Figure 55. Spicules on hyponotum.

Figure 56. Radula, half row.

Figure 57. Major uncinus, posterior and lateral views.

Figure 58. Digestive tract, dorsal view.

See Figures 1–13 for abbreviations.

usually blunt at tip, striated near tip, 45–75 μm in length; isolated bristle (Figure 52) near perinotal margin tipped with minute spicule, ca. 50 μm in length; marginal spicules (Figure 54) long, slender, hyaline, smooth or striated, pointed at tip, 140–185 μm in length; spicules on hyponotum (Figure 55) larger than those of perinotum, hyaline, smooth, rather blunt at tip, 70–115 μm in length; spicules on pallial fold similar to hyponotal spicules, but slightly more slender, 65–80 μm in length and very sparsely set.

Radula (Figures 56, 57, 79): Central tooth roughly oblong in outline with distal cutting edge, slightly swollen at middle of both sides, constricted and thickened posteriorly at bottom, concave at posterior surface, prop plate with round end; centro-lateral with small cusplike projection at outer lateral corner of dorsal edge, posterior portion strongly

projected and reflexed posteriorly, propped by basal plate with obtuse end; major lateral with tridentate cusp; denticles pointed at tip, middle denticle longest, outer one smallest; shaft strongly keeled dorsally, dilated ventrally with prominent swelling inside of anterior portion; inner small lateral solid, much elevated, narrowly extended anteriorly, deeply concave at outer lateral surface; outer small lateral also elevated, roundly sinuated at inner lateral surface, small but rather deeply sinuated at outer lateral surface; major uncinus (Figure 57) slender, spoon-shaped, cusp narrow, rounded at distal end; inner and middle marginals roughly rhomboid in shape, outer marginal squarish, thin, and platelike.

Digestive tract (Figure 58): Stomach pouchlike, blind end situated at bottom or middle of right side of visceral mass;

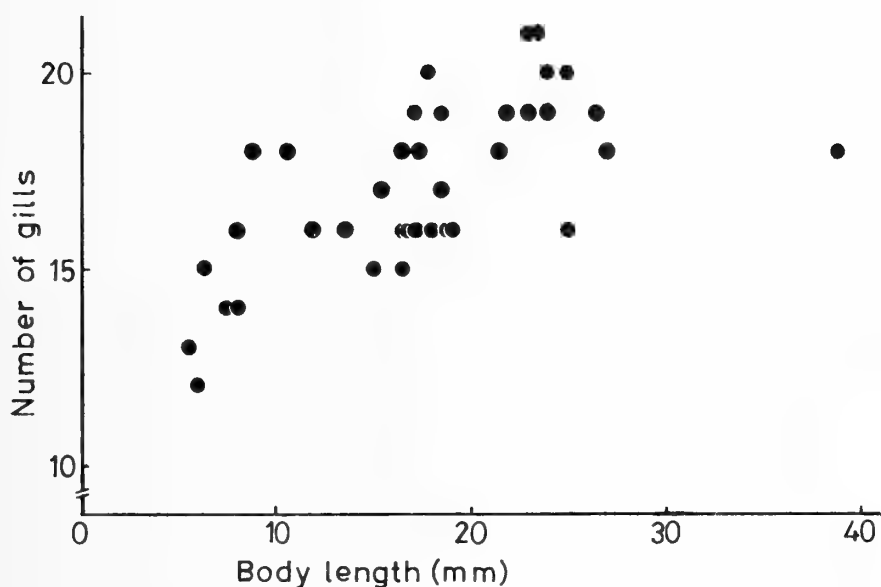


Figure 59

Relationship between body length and number of gills of *Mopalia retifera* ($n = 37$).

anterior intestine originates from left side of stomach, dorsally runs posteriorly to right with U-shaped loop; intestinal valve turns back and connects with posterior intestine; posterior intestine bends three times inside of U-shaped loop of anterior intestine, descends between beginning of anterior intestine and intestinal valve, then turns to right, runs posteriorly, loops one and a half times ventrally and leads back to rectum.

Gills, gonopore, and nephridiopore: Gills merobranchial and abanal, usually extending from under middle of valve III to under posterior margin of valve VII, with number of gills gradually increasing with growth (Figure 59); gonopore typically located between posterior second and third gills and nephridiopore situated one ctenidium behind the gonopore (between two posteriormost gills).

Heart: Heart with one pair of auriculo-ventricular ostia.

Coloration: Preserved valves variable in color, usually brownish or light brown with dark brown stripes along jugal area, but varying from red, orange, yellow to green mottled with irregular spots of various colors; perinotum usually light brown with darker bands; hyponotum uniformly light brown; posterior end of girdle with orange spot which was present in all specimens preserved in alcohol for ten years.

Distribution: Sea of Japan, Pacific coast of Japan from southern part of Hokkaido to Ishigaki Island (25°N), Yellow Sea (Figure 60), on rocks or underside of stones in littoral and sublittoral zones. The deepest record is 70 m in Peter the Great Bay (KLIMOVA & SIRENKO, 1976).

Remarks: This species closely resembles *Mopalia egretta* Berry, 1919, in having regular reticulate sculpture. It is clearly separable from *M. egretta* by the sculptural mesh that narrows like a net pulled longitudinally at the jugal area, and the larger spicules of the setae.

The tegmental sculpture changes with growth. The sculpture of the central area consists chiefly of simple longitudinal riblets in an individual of 6 mm valve length (Figure 50). This sculpture in young individuals is similar to that of a young *Mopalia seta* (Figure 20).

Genus *Plaxiphora* Gray, 1847a

Type species: *Chiton carmichaelis* Gray, 1828 (S.D. by GRAY, 1847b).

Remarks: FERREIRA (1982) stated that the type species of the genus *Plaxiphora* is *Chiton carmichaelis* Gray, 1828, despite the fact that PILSBRY (1893) and subsequent authors considered the type species to be *Chiton auratus* Spawlsky, 1795 (= *Chiton setiger* King & Broderip, 1831). Ferreira indicated that this species was originally designated by GRAY (1847a). However, Gray published three papers in 1847, dated 11 May, 25 May, and 9 November. He created this genus in the first paper (1847a), but the designation was made in the last one (1847b). So, the designation was by subsequent designation, not original designation.

Plaxiphora integra (Is. Taki, 1954)

(Figures 60–72, 77, 82)

Type locality: Okataura, Okago-mura, Hachijo Island, Japan.

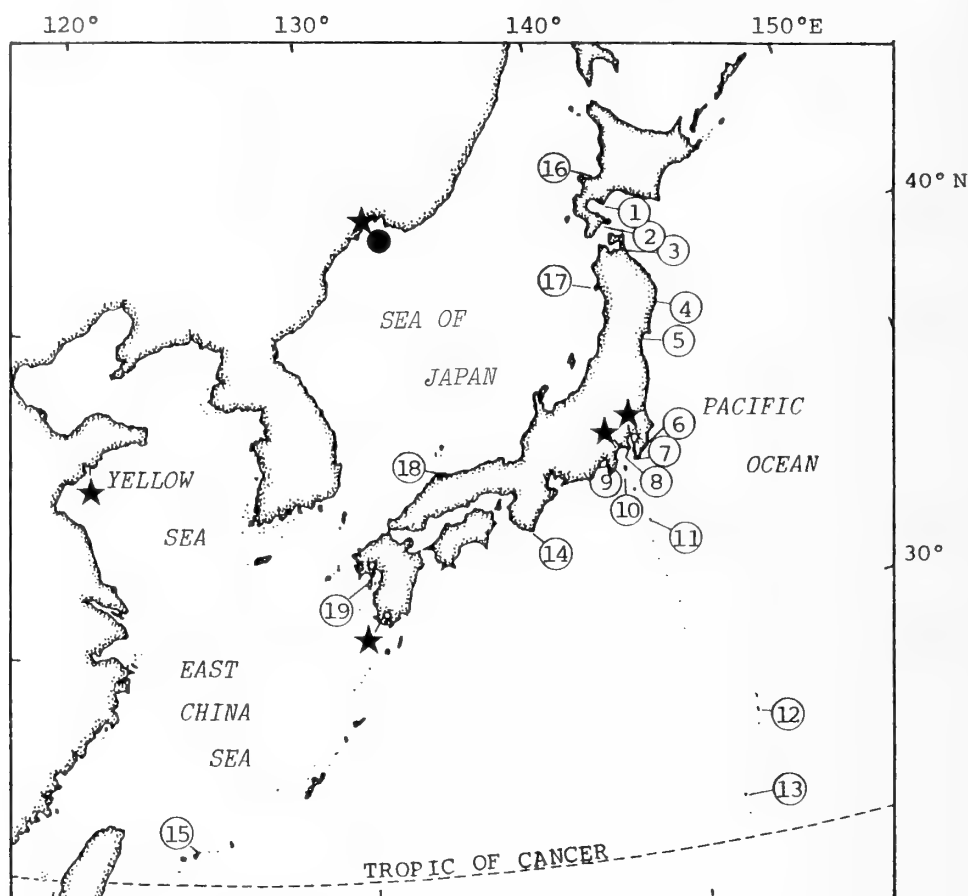


Figure 60

Distribution of *Mopalia retifera* and *Plaxiphora integra*. For *M. retifera*, localities indicated as follows: numbers (1–11 and 14–19), this study (see Table 4); stars, THIELE (1909); solid circle, SIRENKO (1976). For *P. integra*, localities indicated as follows: numbers (11–13), this study (see Table 5) (type locality is 11).

Mopalia (Hachijomopalia) integra IS. TAKI, 1954:60–65, figs. 1–13; IS. TAKI, 1962:33 (name only); IW. TAKI, 1964:411 (name only).

Hachijomopalia integra: IS. TAKI, 1955:202, 205, 207–208 (distribution).

Plaxiphora integra: KAAS & VAN BELLE, 1980:64 (name only); VAN BELLE, 1983:110 (name only).

Material examined: See Table 5.

Description: Animal small, attaining 15 mm in body length, elliptical in outline (Figures 61, 77).

Valves: Head valve (Figure 62) semicircular with eight weakly raised radial ribs; anterior slope slightly convex; tegmental granules oval or somewhat rhomboid, arranged in quincunx and not fused to each other; interior slightly undulated, thickened transversely at middle; insertion plates short, thick, obtuse, thicker at both sides of slit, and anterior surface slightly roughened; slits usually eight in number; eaves narrow, not very spongy; slit rays appear as white lines with some slitlike pores and not grooved.

Intermediate valves (Figure 64) oblong, widest at valve V, slightly beaked, roundly projected at anterior margin of jugal area; side slopes slightly convex; lateral areas raised by two broad ribs; tegmental granules similar to those of head valve but tend to be fused and arranged in longitudinally arching rows in pleural portion of central area; interior smooth, shiny with transverse callus extending from center to near slits; sutural laminae rounded at anterior edge, thin, separated by wide sinus; insertion plates short, not projecting laterally beyond narrow eaves; sutural laminae and insertion plates thickened at both sides of slit; one slit per side; slit rays appear as white lines with minute pores.

Tail valve (Figure 63) small, flat, subtriangular, anterior margin nearly straight; mucro not raised, situated at posterior edge; anterior slope nearly straight; central area ornamented with granules like those of intermediate valves; posterior area very narrow, lying under diagonal ribs of posterior margin; interior with callus along posterior margin; sutural laminae well projected anteriorly with truncate

Table 4
Data of specimens of *Mopalia retifera* used in this study.

Locality*	Collecting depth (m)	Number of individuals	Body length (mm)	Date collected	Collector
Pacific Coast					
1. Muroran	intertidal	5	16.5–29.7	10 Aug. 1983	Y. Kuwahara
Muroran	0–1	2	17.2, 23.5	16 Aug. 1987	H. Saito
2. Hakodate	intertidal	1	21.9	14 June 1987	S. Igarashi
3. Asamushi	intertidal	5	15.4–23.0	5–6 Sep. 1986	S. Murakami
4. Ozuchi	intertidal	1	13.3	June 1987	Y. Kuwahara
5. Miyato	1	1	ca. 24	18 May 1986	H. Saito
6. Kominato	intertidal	1	24.0	10 Apr. 1979	unknown
Kominato	0–1	1	21.5	27 May 1981	unknown
7. Banda	1	1	39.0	26 Apr. 1986	H. Saito
Banda	0–2	2	25.0, 26.4	6–7 June 1986	H. Saito
Banda	intertidal	1	25.9	4 June 1989	T. Okutani
Banda	0	1	ca. 23	17 Feb. 1988	J. Takahashi
8. Aburatsubo	intertidal	4	8.2–11.9	8 Aug. 1986	S. Murakami
9. Shimoda	1	1	16.5	28 May 1986	R. Ueshima
10. Shikine Id.	2	1	13.5	25 Aug. 1987	R. Inoue
11. Hachijo Id.	2–3	3	17.4–21.8	22 Mar. 1987	H. Saito
14. Kushimoto	5	1	10.8	15 Dec. 1987	I. Soyama
15. Ishigaki Id.	0–3	1	ca. 8	Mar. 1976	unknown
Japan Sea					
16. Oshoro	intertidal	1	25.0	29 June 1983	Y. Kuwahara
Oshoro	0–3	7	6.0–17.1	18 Aug. 1987	H. Saito
17. Oga	intertidal	1	ca. 12	21 Aug. 1980	H. Watanabe
18. Katakuni	0.3–0.5	2	15.0, 18.7	27 Mar. 1989	H. Saito
East China Sea					
19. Amakusa	intertidal	1	27.0	19 Mar 1983	S. Nishihama
Amakusa	0	1	17.2	13 May 1987	Y. Takada
Amakusa	0	1	5.6	11 June 1987	Y. Takada

* Locality number corresponds to that in Figure 60.

edge; insertion plate not distinguishable from posterior callus and bearing no slit.

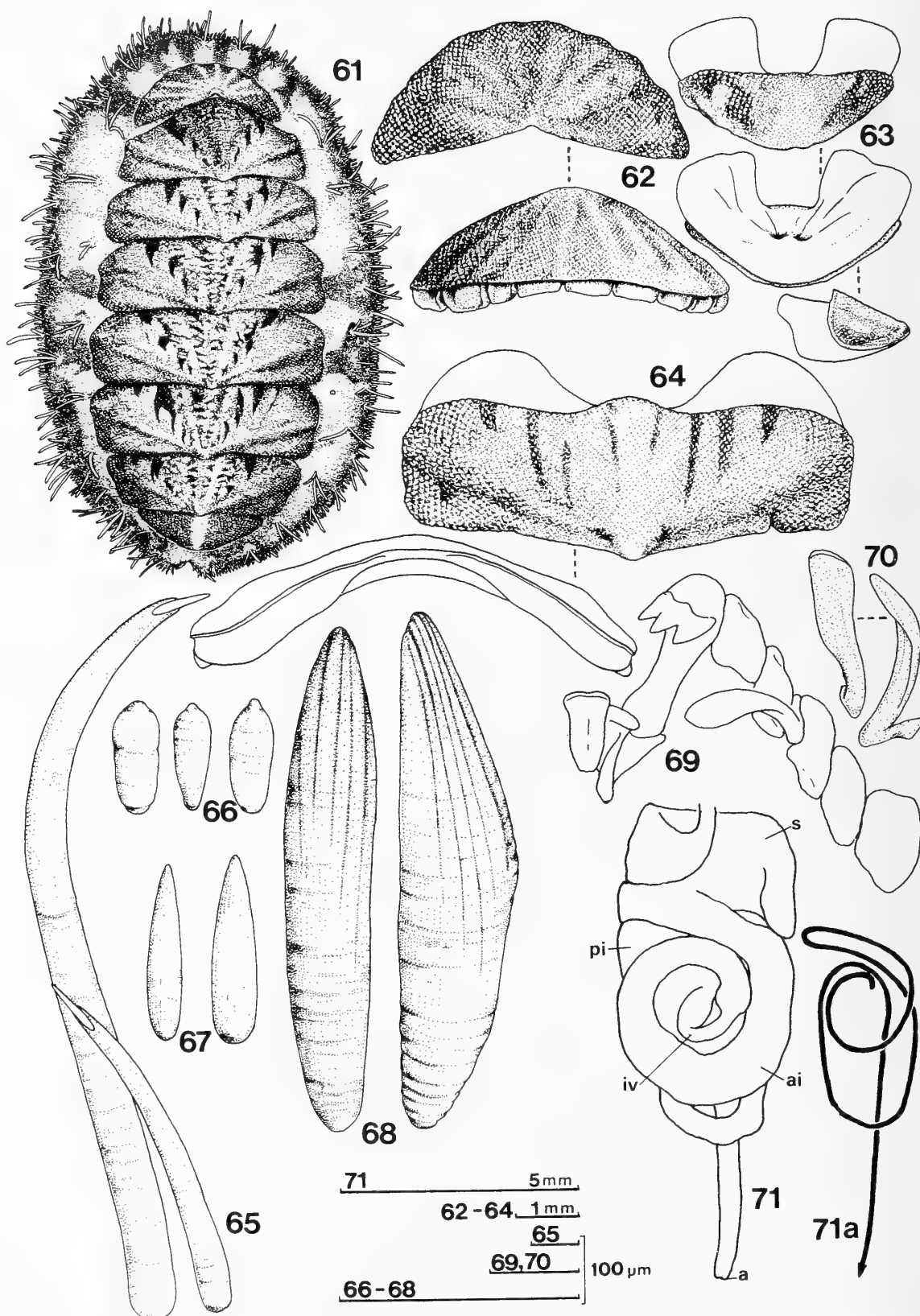
Girdle: Girdle narrow, slightly encroaching at sutures, scarcely sinuated at posterior end; perinotum covered by tufts of bristles and minute spicules; tufts comprised of 2–4 bristles (Figure 65), larger ones on side of sutures and around terminal valves, others gradually becoming smaller toward periphery; each bristle long, up to 1.6 mm in length, light brownish in color, with slender hyaline spicule at distal end; spicules on perinotum (Figure 66) minute, smooth hyaline or brownish in color, blunt at tip, 55–100 μm in length; marginal spicules (Figure 68) long, 265–550 μm in length, striated, hyaline or light brownish in color; spicules on hyponotum (Figure 67) minute, slender, smooth, pointed at tip, hyaline, 85–140 μm in length.

Radula (Figures 69, 70, 82): Central tooth rather small, roughly rectangular, gradually narrowing ventrally, swollen along midline at ventral half on posterior surface with distal arched cusp; centro-lateral with prominent cusp at lateral corner of dorsal edge, anterolaterally propped by well-projected basal plate; major lateral with long keeled

shaft and tridentate cusp; denticles are nearly equal in size, rather blunt; inner small lateral solid, elevated, posterior surface moderately sinuated; outer small lateral elevated and roughly rhomboid-shaped; major uncinus (Figure 70) spoon-shaped with rather long cusp; inner and middle marginals thick and platelike; outer marginal large, thin, and platelike.

Digestive tract (Figure 71, 71a): Stomach pouchlike, broad, blind end situated at right side of visceral mass; anterior intestine originates from left side of stomach, runs posteriorly to right, loops one and a quarter turns dorsally; intestinal valve bends and connects anteriorly with posterior intestine; posterior intestine runs along inside of anterior intestine, descends ventrally behind beginning of anterior intestine, then turns to right, revolves one and a half times ventrally, and leads back to rectum.

Gills, gonopore, and nephridiopore: Gills holobranchial and abanal, anteriormost gill situated under posterior margin of valve II, extending for about $\frac{1}{5}$ of foot length, with the number increasing with growth (Figure 72); gonopore located between posterior second and third gills, and ne-



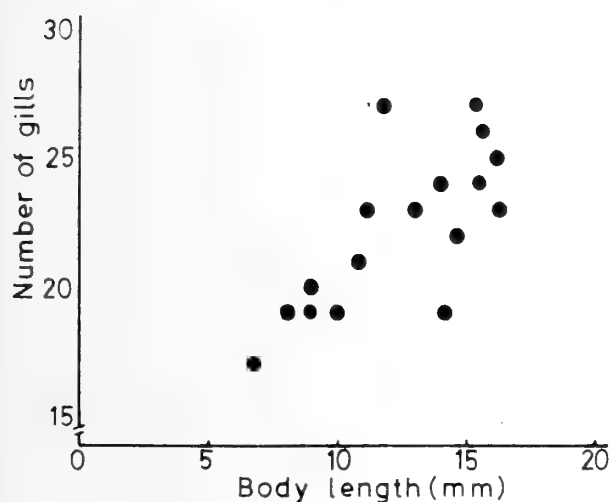


Figure 72

Relationship between body length and number of gills of *Plaxiphora integra* ($n = 17$).

phridiopore situated one ctenidium behind the gonopore (between two posteriormost gills).

Heart: Pericardium extending to boundary between valves V and VI; heart with two pairs of auriculo-ventricular ostia.

Coloration: Preserved valve whitish with dark brownish wedge-shaped patterns in central area and mottled with brown, yellow, green, blue-green, or pink; girdle light brown with brownish bands; hyponotum uniformly light brown.

Distribution: Hachijo Island and Ogasawara Islands (Figure 60), usually found on well-exposed rocks covered by coralline algae or on coralline-covered rocks in high

intertidal tidepools. This species has been known only from the type locality, Hachijo Island (33°N). The present report extends the known range of distribution southward to the Ogasawara Islands (25°N).

Remarks: IS. TAKI (1954) created the subgenus *Hachijomopalina* for this species which he believed to be a *Mopalina*. He distinguished this subgenus from *Mopalina* s.s. by the absence of slits in the tail valve and from *Plaxiphora* by the absence of a spicule at the tip of the bristles. But, features of this species such as the granular surface of the tegmentum, slitless tail valve, and bunched bristles are not those of the genus *Mopalina* but rather of the genus *Plaxiphora*. KAAS & VAN BELLE (1980) and VAN BELLE (1983) previously transferred this species from *Mopalina* to *Plaxiphora*, but without discussion. Their treatment is quite appropriate because the spicules of the bristles were observed in this study. No generic difference is found between this species and species of the genus *Plaxiphora*.

This species is related to a small-sized species group of *Plaxiphora* known from tropical and subtropical waters of the Pacific and Indian oceans: namely, *Plaxiphora parva* Nierstrasz, 1906, *P. obscurellus* (Souverbie & Montrouzier, 1866) [= *P. primordia* (Hull, 1924) fide STRACK (1986)], *P. kamehamehae* Ferreira & Bertsch, 1979, *P. dardennei* Leloup, 1981, *P. tulearensis* Leloup, 1981, and *P. gweniaie* Ferreira, 1987. Among these, *Plaxiphora integra* seems to bear closest resemblance to *P. kamehamehae*. In fact, it is rather difficult to distinguish these two species. However, they are separated by a few characters, such as the higher dorsal ridge and longer tail valve in *P. kamehamehae*. The higher dorsal ridge may be caused by a difference in their habitat; *P. integra* lives chiefly on well-exposed, intertidal rock surfaces covered with coralline algae, whereas *P. kamehamehae* occurs in "<1 metre of water, attached to the sides of dead coral pieces, usually occupying a depression

Explanation of Figures 61 to 71

Figures 61–71. *Plaxiphora integra* (Is. Taki, 1954). Figure 61. body length 16.2 mm. Figures 62–70. body length 15.5 mm. Figure 71. body length 15.6 mm, from Hachijo Island.

Figure 61. Dorsal view of animal.

Figure 62. Head valve, dorsal and anterior views.

Figure 63. Tail valve, dorsal, ventral, and lateral views.

Figure 64. Valve IV, dorsal and anterior views.

Figure 65. Bristles.

Figure 66. Spicules on perinotum.

Figure 67. Spicules on hyponotum.

Figure 68. Marginal spicules.

Figure 69. Radula, half row.

Figure 70. Major uncinus, posterior and lateral views.

Figure 71. Digestive tract, dorsal view.

Figure 71a. Diagram of the course of posterior intestine.

See Figures 1–13 for abbreviations.

Table 5
Data of specimens of *Plaxiphora integra* used in this study.

Locality*	Collecting depth (m)	Number of individuals	Body length (mm)	Date collected	Collector
11. Hachijo Id.	intertidal	12	8.1–16.2	5 Mar. 1988	H. Saito, K. Tsuchiya
12. Chichijima Id.	intertidal	10	6.8–16.3	1–3 July 1989	H. Saito & K. Tsuchiya
13. Iwojima Id.	intertidal	1	ca. 13	July 1985	K. Nishimura

* Locality number corresponds to that in Figure 60.

or pit" (FERREIRA & BERTSCH, 1979). Even though the morphological differences between Japanese and Hawaiian species are meagre, we believe that speciation has proceeded with differentiation of water masses of the Pacific. The sporadic occurrence of other similar-looking species localized in small geographic areas of the Indo-Pacific may also be interpreted as evidence of a radiation from the common ancestor.

The type specimens of this species are in the private collection of the Takis in Kyoto, inherited from the late Drs. Isao and Iwao Taki.

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shihama and Yoshitake Takada, Kyushu University; Kazuhisa Nishimura, Tokyo Fisheries Experimental Station; Dr. Boris Sirenko, Academy of Sciences, Leningrad; Isamu Soyama, Fujisawa City; Mr. Hermann Strack, Rotterdam; Mrs. Ryoko Tsubokawa (née Inoue), Messers Hideki Numanami, and Kotaro Tsuchiya, Tokyo University of Fisheries; Rei Ueshima, Tsukuba University; Hiroki Watanabe, Oga City.

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Explanation of Figures 73 to 82

Figure 73. *Mopalia middendorffii* (Schrenck, 1861). Body length 28.1 mm, from Oshoro.

Figure 74. *Mopalia schrencki* Thiele, 1909. Body length 15.6 mm, from Kitami-esashi.

Figure 75. *Mopalia seta* Yakovleva, 1952. Body length 44.3 mm, from Hiroo.

Figure 76. *Mopalia retifera* Thiele, 1909. Body length 16.5 mm, from Shimoda.

Figure 77. *Plaxiphora integra* (Is. Taki, 1954). Body length 16.2 mm, from Okataura, Hachijo Island.

Figure 78. *Mopalia schrencki* Thiele, 1909. Body length ca. 20 mm, from Rausu. SEM photograph of radula. Scale bar: 100 μ m.

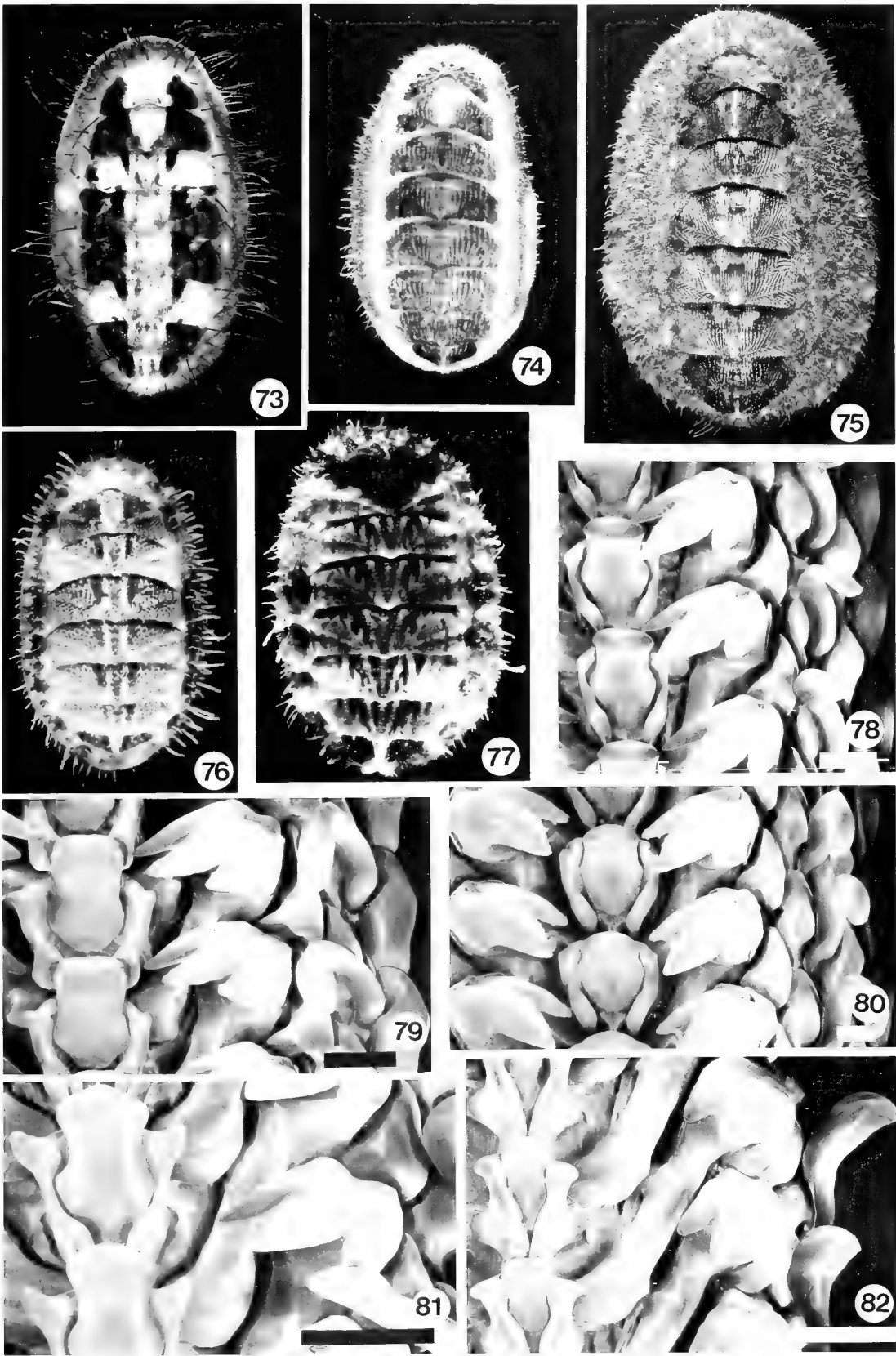
Figure 79. *Mopalia retifera* Thiele, 1909. Body length 23.5 mm, from Muroran. SEM photograph of radula. Scale bar: 100 μ m.

Figure 80. *Mopalia seta* Yakovleva, 1952. Body length ca. 36 mm, from Muroran. SEM photograph of radula. Scale bar: 100 μ m.

Figure 81. *Mopalia middendorffii* (Schrenck, 1861). Body length 16.9 mm, from Oshoro. SEM photograph of radula. Scale bar: 100 μ m.

Figure 82. *Plaxiphora integra* (Is. Taki, 1954). Body length 15.5 mm, from Okataura, Hachijo Island. SEM photograph of radula.

Scale bar: 100 μ m.



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Helicoradomenia juani gen. et sp. nov., a Pacific
Hydrothermal Vent Aplacophora
(Mollusca: Neomeniomorpha)

by

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Abstract. The aplacophoran *Helicoradomenia juani* gen. et sp. nov. is found in large numbers at the northeast Pacific vent sites of Juan de Fuca Ridge, Explorer Ridge, and Gorda Ridge. It is placed in the family Simrothiellidae on the basis of radular morphology (distichous bars with paired ventral pockets) and is separated from other genera in the family by the presence of solid epidermal spicules.

INTRODUCTION

Several closely related species of neomenioid (footed) Aplacophora occur at hydrothermal vents. They were originally assigned to the genus *Simrothiella* Pilsbry, 1878 (SCHELTEMA, 1988; TURNER, 1985, through personal communication from Scheltema), but re-examination of type material of *S. margaritacea* (Koren & Danielssen, 1877) indicates that the latter is generically distinct from the hydrothermal vent species on the basis of the radula alone (cf. Figure 2D, E). The type species for the new genus is described here.

MATERIALS AND METHODS

All specimens (365) were collected from the Endeavour segment of Juan de Fuca Ridge (47°57'N, 129°04–06'W, 2250 m), Explorer Ridge (49°46'N, 130°16'W, 1800 m), and Gorda Ridge (41°00'N, 127°30'W, 3271 m) from the deep submersible research vessels *ALVIN* and *PISCES*.

About 20 specimens were dissected or sectioned. Radulae, epidermal spicules, and copulatory spicules were dissociated from dissected anterior or posterior ends of specimens by dissolving tissue in hypochlorite solution (household bleach) or, for some radulae, in 10% NaOH solution. They were washed and placed in a drop of glycer-

ine for camera lucida drawing. After further washing, permanent slides were made of air-dried spicules and CMCP-10 (TURTOX)-mounted radulae. One specimen was prepared for histology by decalcifying the spicules with 0.5 M EGTA overnight, dehydrating in dimethoxy propane, and embedding in epon/araldite epoxy resin. Sections were cut at 1.5 μ m and stained with Richardson's stain (azure II and methylene blue). Standard paraffin sections (7 μ m) were also cut and stained with Mallory-Heidenhain trichrome. Types are deposited in the National Museum of Natural History (NMNH), Washington, DC.

Terminology: *Skeletal* (=tangential) spicules are those that lie within the cuticle and spiral around the body at a 45° angle, crossing each other at 90°; *upright* (=radial) spicules extend out of the cuticle; *isochromes* are boundaries between color bands produced in solid spicules by cross-polarized light; *distichous* refers to a radula formed by repeated rows of two teeth each (formula: number of rows \times 1·1); *denticulate bar* is a bar-like radular tooth with denticles on the side opposite to the attachment of the tooth to the radular membrane; *vestibule* (=atrium) is the anterior cavity that lies above the mouth either united with or separate from the mouth opening and that contains sensory papillae; *oral cavity* (=buccal cavity) is the ventral space into which the mouth opens and which leads dorsally to the pharynx.

SYSTEMATICS

Subclass Neomeniomorpha Pelseneer, 1906

Ventroplicida Boettger, 1956

Solenogastres Gegenbaur, 1878 (*partim*), Salvini-Plawen, 1967

Aplacophoran mollusks with a narrow foot in a ventral furrow, an anterodorsal vestibule with sensory papillae, a combined stomach-midgut gland, serial lateroventral muscles, a mantle cavity without ctenidia, and paired hermaphroditic gonads.

Family SIMROTHIELLIDAE

Salvini-Plawen, 1978

Type species: *Solenopus margaritaceus* Koren & Danielsen, 1877.

Radula with distichous denticulate bars and short or long paired anteroventral radular pockets; spicules hollow or solid; skeletal spicules present or absent; morphology of ventral salivary glands varied.

Helicoradomenia Scheltema & Kuzirian,
gen. nov.

Plump to somewhat elongate, nearly smooth to spiny, 5 mm or less in length, dorsoposterior sense organ and sometimes dorsofrontal sensory pit present; proboscis large, protrusible; mouth at proximal end of vestibule; pedal pit large, often protruded; cuticle thin, epidermal glands not stalked; spicules solid, upright, skeletal spicules lacking; radula large, lateral denticles longest; radula spiraling into paired anteroventral radular pockets, first-formed teeth not retained; paired ventral salivary glands small, opening through paired ducts; paired sac-like seminal receptacles; single gametopore; copulatory spicule pockets paired, 2 or more long spicules per pocket; mantle cavity with long respiratory papillae.

Range: Eastern and western Pacific hydrothermal vents.

Etymology: *helico* = helical, *rad* = abbreviation for radula, *menia* = moon, usual ending for neomenioid ("new moon") aplacophorans.

Helicoradomenia juani Scheltema & Kuzirian,
sp. nov.

(Figures 1–5)

Holotype: 3.4 mm long, anterior diameter 0.7 mm, midbody 1.0 mm, posterior 1.6 mm. Endeavour Segment, Juan de Fuca Ridge, 47°57'N, 129°04'W, 2250 m (DSRV *ALVIN* Dive 1419). NMNH No. 836328.

Figured paratypes: Nos. 1, 3, 6, 9, 14, from type locality. NMNH Nos. 860188, 860187, 860191, 860189, and 860190, respectively.

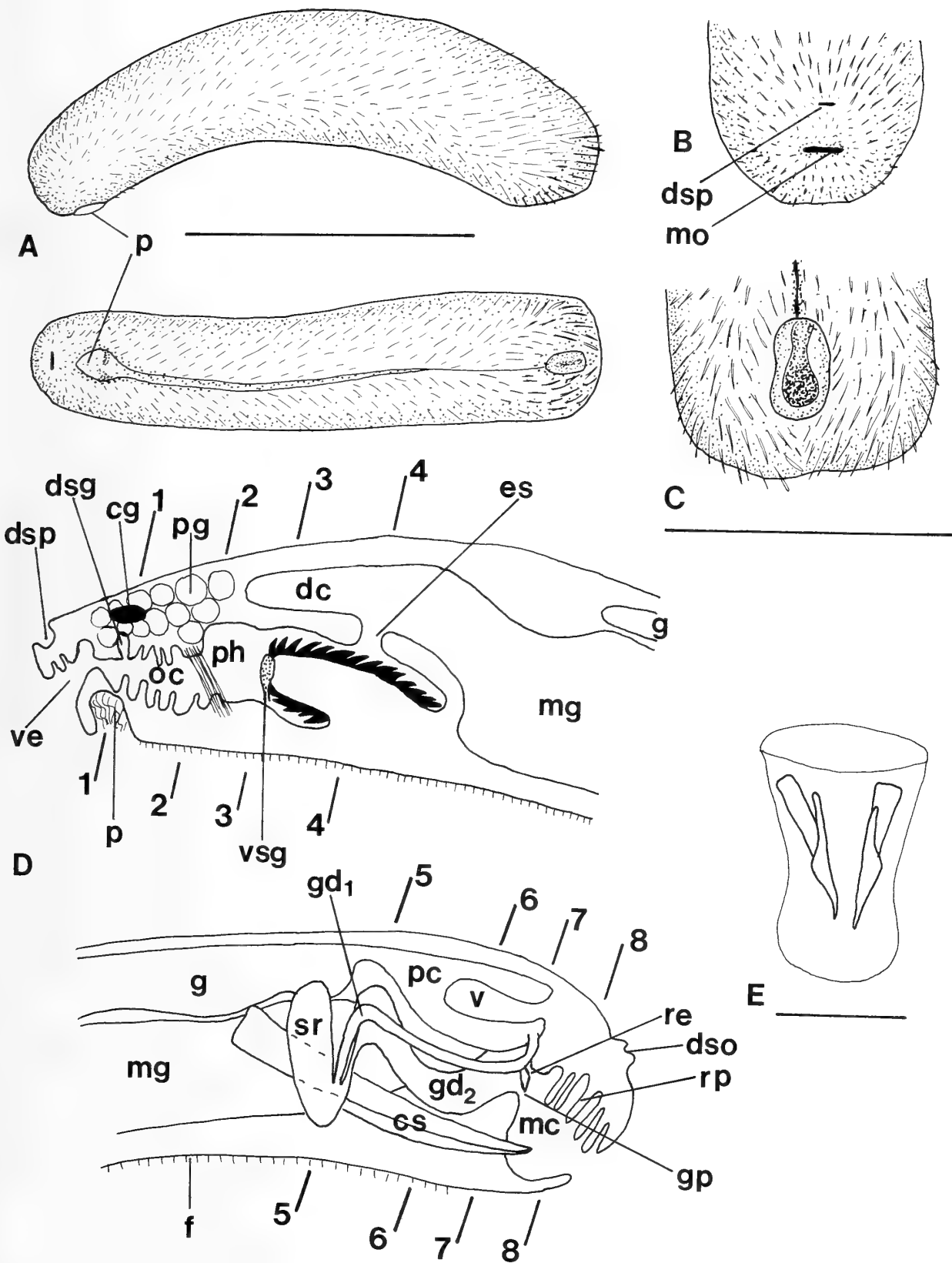
Distribution: Explorer, Juan de Fuca, and Gorda ridges, 1800–3271 m.

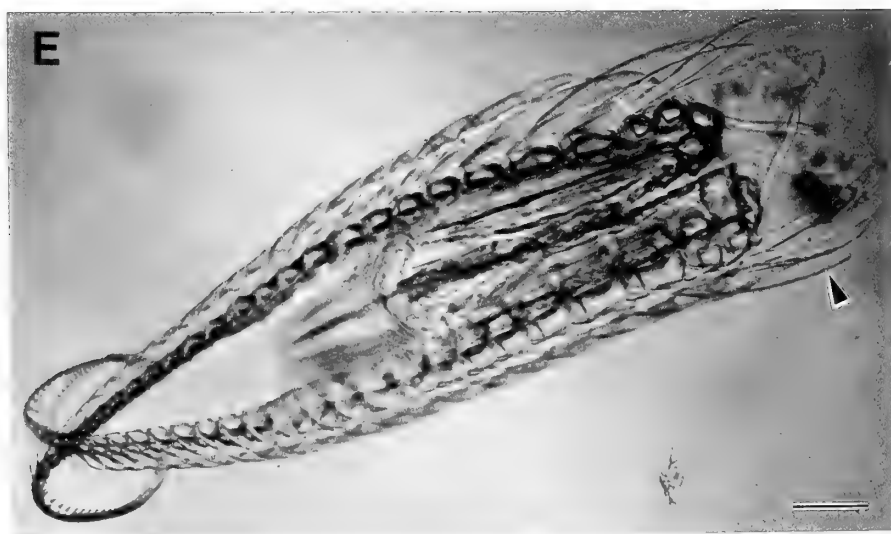
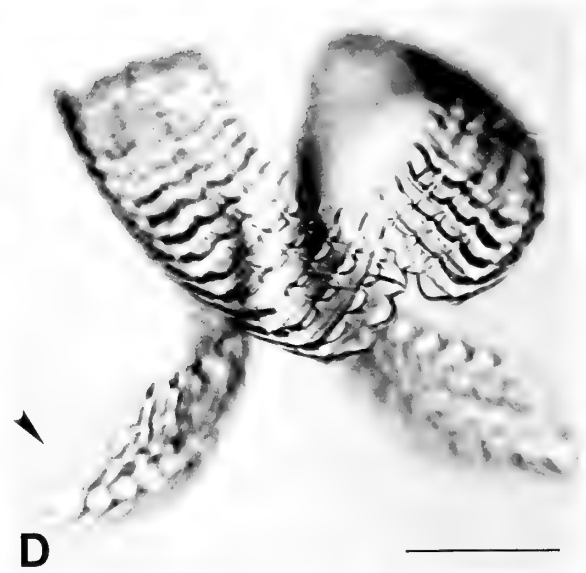
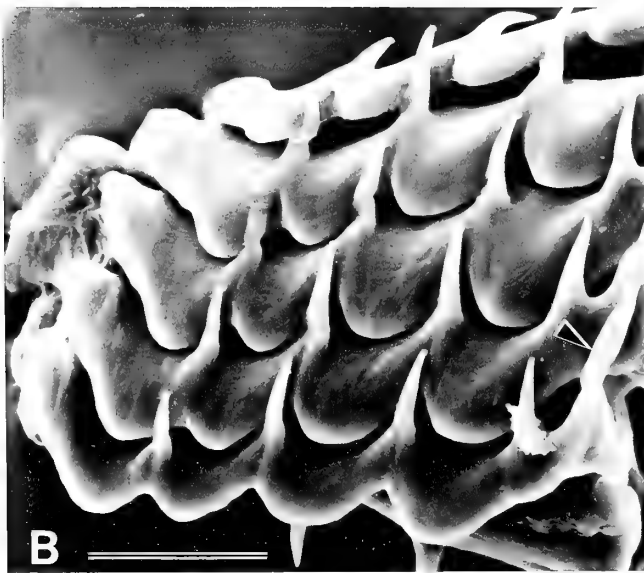
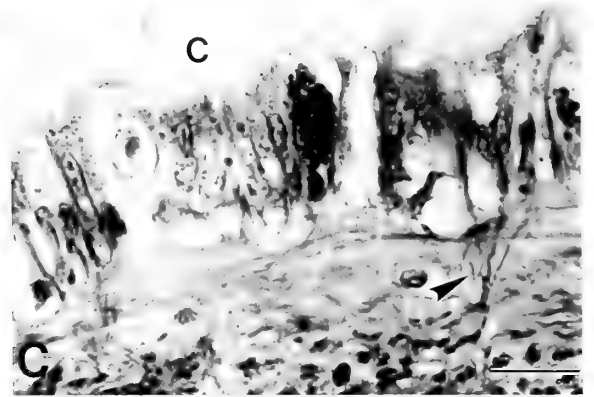
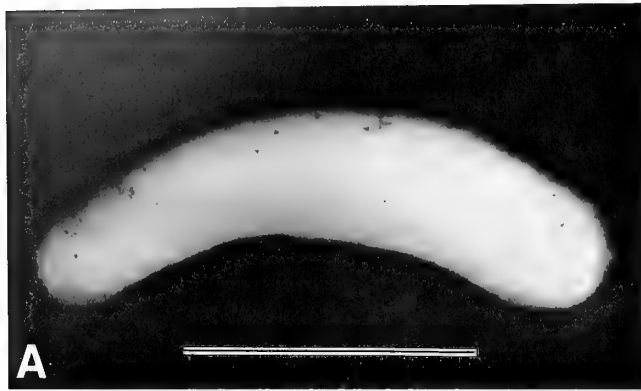
Diagnosis: Appearance fuzzy, length to 5 mm, narrowest anteriorly, mean index (length : diameter) at midbody 4:1; with dorsofrontal sensory pit; spicules widest at base and distally pointed, varying from short, wide, and recurved (110 μ m long, 18 μ m wide, 10 μ m thick) to long, slender and curved (200 μ m long, 14 μ m wide, more than 10 μ m thick); radular formula 34–35 \times 1.1, teeth with 5 or 6 denticles, lateral denticle twice length of next adjacent one; 2 spicules per copulatory spicule pocket, curved, sharply pointed distally, up to 1 mm long, shorter spicule of pair with proximal process; accessory copulatory spicules 2 on each side, with 3 low bumps.

External anatomy and hard parts: Body (Figures 1A–C, 2A) somewhat elongate, index at midbody 3–4:1; anterior end rounded; wider posterior end slightly pointed with flattened ventral region around mantle cavity opening; mouth slit lateral; dorsofrontal sensory pit obvious as lateral slit; dorsoterminal sense organ not evident externally; mantle cavity opening axial, oval. Epidermal spicules (Figure 3A, B) of 5 types, longest at posterior end of body, usually thickest near base: (1) evenly curved, narrow, width even except tapered distally to point, up to 130 μ m long \times 11 μ m wide, 7 μ m to more than 10 μ m thick, grades into (2) straight or evenly curved, width even except expanded basally and tapered distally to blunt point, up to 200 μ m long \times 15 μ m wide, more than 10 μ m thick; (3) broad, base recurved proximal to indentation or unevenly curved, distally tapered to point, up to 112 μ m long \times 18

Figure 1

Helicoradomenia juani gen. et sp. nov. A: Holotype, showing spicule orientation and somewhat protruded pedal pit, lateral (above) and ventral views. B: Holotype, anterior end, frontal view showing relationship of dorsofrontal sensory pit and opening to mouth and vestibule. C: Holotype, posterior end, ventral view, with oval-shaped mantle cavity opening. D: Schematic sagittal sections of anterior (above) and posterior ends; transverse sections 1–8 are keyed to histologic sections in Figures 4 and 5. E: Copulatory spicules *in situ*, paratype no. 3, ventral view of posterior end (rotated 90° from D, mantle opening below), tissue partially dissolved. Key: cg, cerebral ganglion; cs, copulatory spicule; dc, dorsal cecum; dsg, dorsal salivary gland; dso, dorsoterminal sense organ; dsp, dorsofrontal sensory pit; es, esophagus; f, foot; g, gonad; gd_{1,2}, upper and lower gametoducts; gp, gametopore; mc, mantle cavity; mg, midgut (stomach-intestine); mo, opening to vestibule and mouth; oc, oral cavity; p, pedal pit; pc, pericardial cavity; pg, pedal gland; ph, pharynx; re, rectum; rp, respiratory papilla; sr, seminal receptacle; v, ventricle; ve, vestibule; vsg, ventral salivary gland. Scale bars: A = 2.0 mm, B, C = 1.0 mm, E = 0.05 mm.





μm wide, 9 μm or less thick; (4) short, straight, rounded basally, tapered distally to point, up to 74 μm long \times 15 μm wide, 7 μm or less thick; (5) short, straight or curved, distally pointed, base straight, up to 80 μm long \times 11 μm wide, 9 μm or less thick. Pedal-groove spicules short and broad, up to 70 μm long \times 16 μm wide, 4–5 μm thick.

Copulatory spicules (Figures 1D, E, 3D, E, 5C) 2 per pocket, curved dorsally, sharply pointed distally, longer spicule up to 1 mm in length with straight base, shorter spicule with proximal process, medioventral to and partially wrapped around longer spicule. Paired accessory spicules (Figures 3C, 5G) 2 on each side, recurved, each with 3 low bumps on base.

Radula (Figures 2B, D, 3F, G) with single turn into ventral pockets; 34 or 35 rows; teeth with 5 or 6 denticles, lateralmost denticle twice length of next adjacent denticle; bar about 115 \times 12 μm , lateral denticle 30 μm ; dimensions of older teeth smaller.

Internal anatomy (Figure 1D): Cuticle 22 μm thick. Epidermis (Figure 2C) 22 μm thick, with more than one type of secretory cell, pierced by tubules from hemocoel. Body-wall musculature well developed. Pedal pit lined by large secretory cells (Figure 4A). Vestibule with few low, broad papillae; cirri grouped at mouth opening with which vestibule is united. Oral cavity deeply folded, also with cirri (Figure 4A). Multicellular dorsal salivary gland small (Figure 4A). Pharyngeal wall smooth (Figure 4B). Ventral salivary glands paired, small, tube-shaped, multicellular, unbranched, non-basophilic staining (Orange G), each opening through separate duct into anterior end of anteroventral radular pocket (Figure 4C). Anteroventral radular pocket as paired pouches which remain connected medially for some distance (Figure 4C). Radula bolsters large, bolster muscles well developed (Figure 4D). Short esophagus present (Figure 4D). With single, short dorsal midgut cecum (Figure 4D); midgut sacculate. Pericardial cavity large (Figure 5C); heart large, free within pericardium, opening from a posterior dorsal sinus (Figure 5C, D). Seminal receptacles as paired, large tubes lying in a dorsoanterior to ventroposterior position, each opening through a narrow tube leading dorsally to lower gametoduct (Figure 5A, B). Upper gametoduct opens into sem-

inal receptacle through a narrow duct adjacent to the tube joining the seminal receptacle and lower gametoduct (Figure 5B). Gametopore single, opening into mantle cavity below rectum (Figure 5E). Mantle cavity with numerous long respiratory papillae (Figure 5F). Dorsoterminal sense organ large, papillate, seen only in sectioned material.

Remarks: The reproductive system of these animals is unusual because (1) the upper gametoduct is joined to the distal end of the seminal receptacle rather than to the lower gametoduct, and (2) the position of the tubes connecting the seminal receptacles to upper and lower gametoducts is asymmetrical, being medial to the copulatory spicules on the left side and lateral to them on the right side in the specimen sectioned (Figure 5A, B).

The ventral salivary glands are embedded in the muscles of the radula (Figure 4C). They are unusually small and do not have a basophilic reaction to trichrome staining. This condition is atypical from the strong basophilia found in the salivary glands of most other neomenioids and presumably reflects diet. Nematocysts were not found in the midgut of *Helicoradomenia juani*, and Cnidaria did not occur where this species was collected. It is thus assumed that *H. juani* is not a cnidarivore as are most neomenioids. The organic matter seen in the gut has not been identified.

Relationships: Isolated radulae have been examined from three genera belonging to the family Simrothiellidae Salvini-Plawen: *Simrothiella* Pilsbry, 1898 (Figure 2E), *Kruppomenia* Nierstrasz, 1903a (synonymy with *Simrothiella*, SALVINI-PLAWEN, 1978, in error), and a new genus to be published which will include "*Simrothiella*" *schizoradulata* Salvini-Plawen, 1978. All have distichous bars and short to very long paired anteroventral radular pockets. It is this radular morphology that is the basis for placing *Helicoradomenia* in the Simrothiellidae. The epidermal spicules provide a basis for generic separation. In *Helicoradomenia* they are solid and thus differ from the hollow spicules found in all other genera in the family, which also includes *Cyclomenia* Nierstrasz, 1902, *Uncimania* Nierstrasz, 1903b, *Birasoherpia* Salvini-Plawen, 1978, *Biseramenia* Salvini-Plawen, 1968, and *Sialoherpia* Salvini-Plawen, 1978. Although the illustrated radulae of these

Figure 2

A–D. *Helicoradomenia juani*. A: Holotype, anterior to left (cf. Figure 1A). B: Scanning electron photomicrograph of part of left half of radula from above, medial edge to left, paratype no. 6; five rows of teeth, some with five and some with six denticles, shown. Arrowhead indicates longest, most lateral denticle. C: Light micrograph of histologic section of epidermis and cuticle (c) of mantle showing various gland cells and innervation by nerve fibers (arrowhead). D: Light micrograph of entire radula from below showing helical position of teeth from anteroventral radular pocket, paratype no. 14; newest tooth indicated by arrowhead. E. Light micrograph of radula of *Simrothiella margaritacea* (Koren & Danielssen, 1877), ventral view with elongated paired ventral radular pockets to left and long lateral teeth (arrowhead) extending into pharynx on right (R. V. Chain 106 Stn 316, 50°58.7'N, 13°01.6'W, 2173 m). Species determination from comparison with radula isolated from a syntype, Bergen Museum no. 2078. Scale bars: A = 2.0 mm; B, C = 0.02 mm; D, E = 0.1 mm.

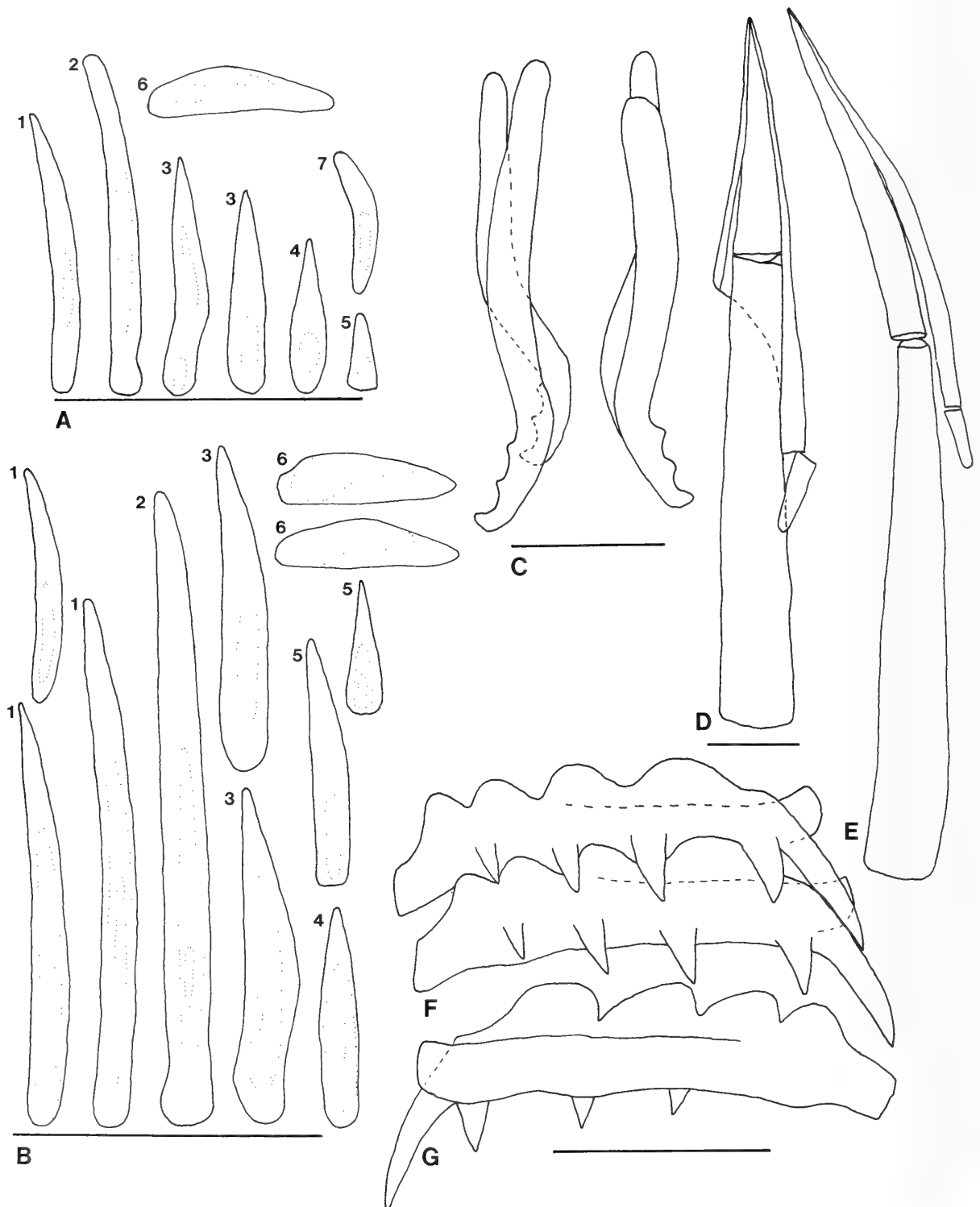


Figure 3

Helicoradomenia juani, hard part morphology. A, B: Epidermal spicules, anterior and posterior, respectively, paratype no. 1; selected isochromes indicated by dotted lines; 1–5, see text; 6, pedal-groove spicules; 7, oral spicule. C: Accessory copulatory spicules, paratype no. 1 (cf. Figure 5G). D, E: Copulatory spicules from paratype nos. 1 and 9, respectively. F: Two adjacent teeth from right side of radula, paratype no. 1. G: Single radular tooth, right side, paratype no. 1, view from beneath radular membrane showing bar. Scale bars: A, B, D, E = 0.1 mm; C, F, G = 0.05 mm.

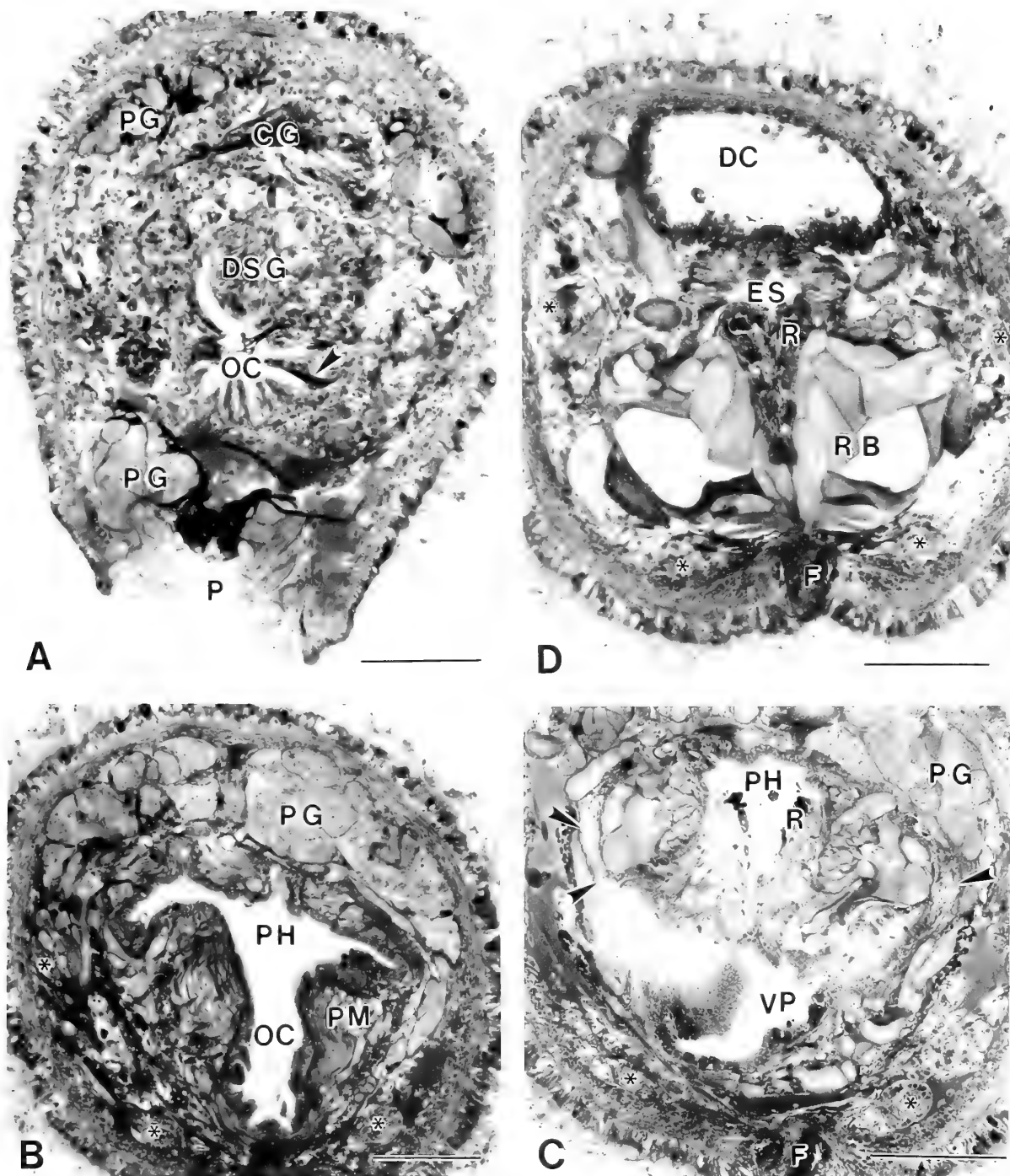
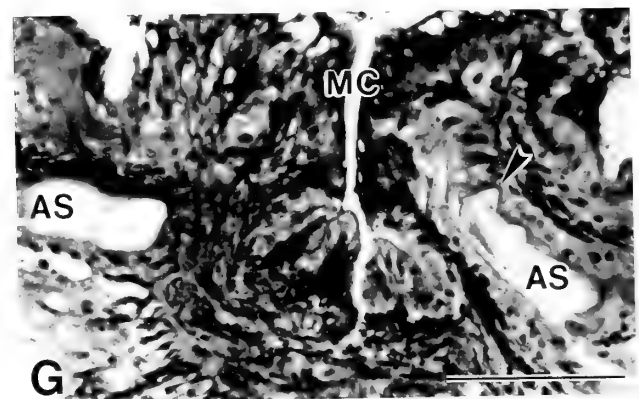
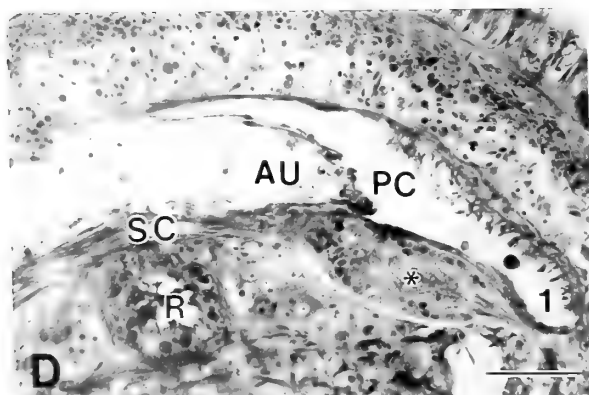
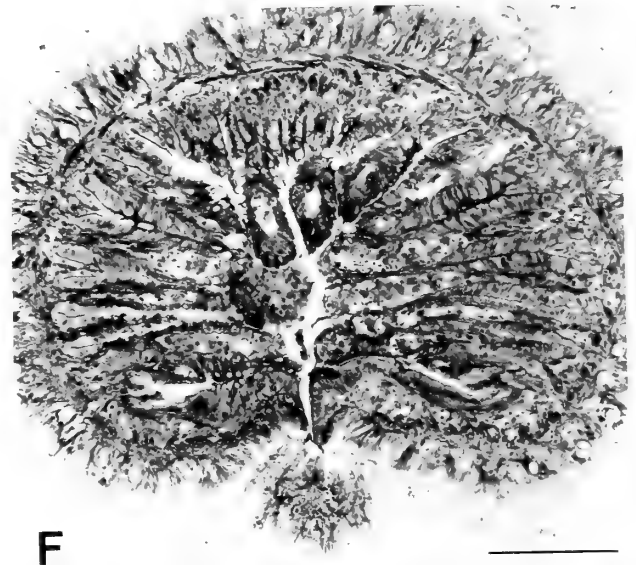
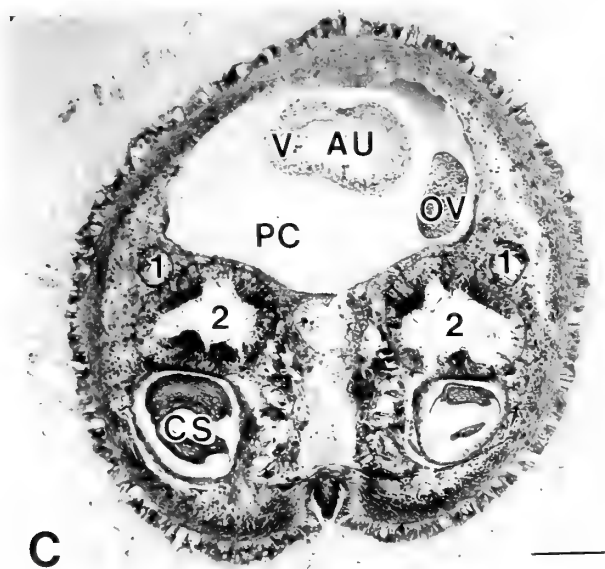
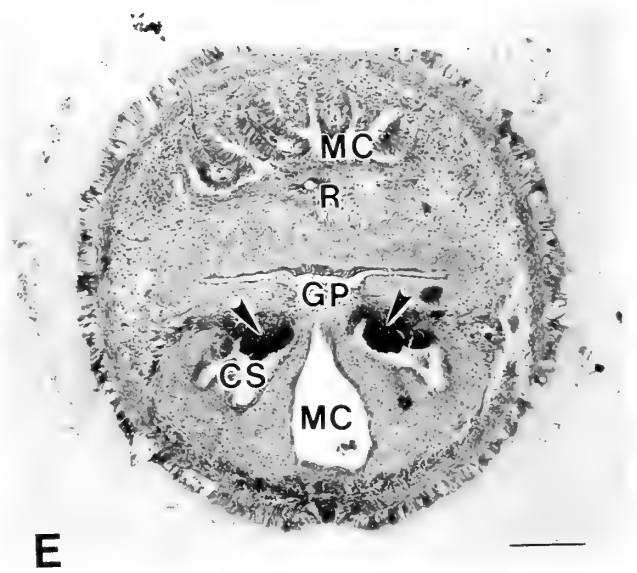
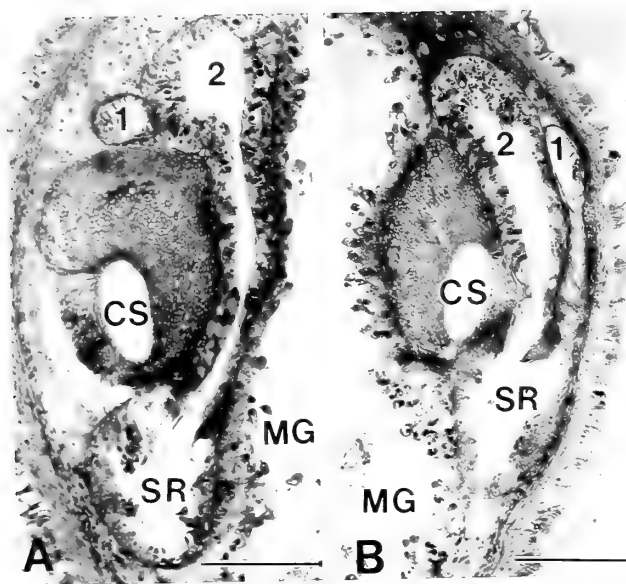


Figure 4

Anterior end, *Helicoradomenia juani*, transverse histologic sections 1 through 4 of Figure 1D. A: Section 1 through cerebral ganglion, dorsal salivary gland, oral cavity with cirri (arrowhead), and pedal pit. B: Section 2 through oral cavity, pharynx, and pharyngeal muscles. C: Section 3 through paired ventral salivary glands (arrowheads), gland on left shown opening into anteroventral radular pocket. D: Section 4 through dorsal cecum of midgut, esophagus, radula and radula bolster with well-developed musculature and large chondroid-like cells. Key: CG, cerebral ganglion; DC, dorsal cecum; DSG, dorsal salivary gland; ES, esophagus; F, foot; OC, oral cavity; P, pedal pit; PG, pedal gland; PH, pharynx; PM, pharyngeal muscle; R, radula; RB, radula bolster; VP, anteroventral radular pocket. Asterisks indicate ganglia of lateral and anteroventral nerve cords. Scale bars: A-D = 0.1 mm.



latter five genera are drawn from sectioned material only, they all appear to be distichous denticulate bars.

SALVINI-PLAWEN (1978) placed the family Simrothiellidae in the order Cavibelonia, a grouping based on possession of hollow spicules. *Helicoradomenia* is the second genus with solid spicules to be placed in a cavibelonid family. The genera of Pararrhopalidae, if brought together on the basis of possessing fishhook-shaped spicules, also form a cavibelonid family with both solid (*Ocheyoherpia*) and hollow spicules (SCHELTEMA, in press). The families of Cavibelonia vary in respect to type of radula and ventral salivary glands and in presence or absence of skeletal spicules (SALVINI-PLAWEN, 1985). The morphologies of these structures are not unique to the Cavibelonia but are found in other orders as well. We therefore conclude that the order Cavibelonia is polyphyletic and needs to be revised. The family Simrothiellidae should probably be raised to ordinal level, but not until further comparisons of newly collected material have been made.

Distribution: Several vent species of *Helicoradomenia* still to be described occur at other rift sites in the eastern Pacific other than those off the northwest United States where *H. juani* is found: off the Galápagos (2 species), at 13°N (1 species), at 20°N (3 species, one in common with Galápagos), and from Gorda Ridge (1 species). The genus has also been collected from western Pacific rift sites in the Marianas Back Arc and Lau basins. None of these species has been collected in such high numbers as *H. juani*.

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Figure 5

Posterior end, *Helicoradomenia juani*, transverse histologic sections 5 through 8 of Figure 1D. A, B: Section 5, left and right sides, respectively, showing the connections between the upper and lower gametoducts and the paired seminal receptacles; position of ducts on left side lies between copulatory spicules and midgut, whereas those on right lie lateral to the copulatory spicules. C: Section 6 through pericardium with ovum, heart, upper and lower gametoducts, and copulatory spicule pockets. D: Section 7 through posterior end of pericardial cavity where it connects to upper gametoduct, beginning of auricle, rectum and suprarectal commissure arising from large ganglion of the lateral nerve cord (asterisk). E: Unnumbered section between sections 7 and 8 through proximal end of mantle cavity just anterior to openings of rectum and gametopore and through the copulatory spicule glands (arrowheads). F: Section 8 through mantle cavity with long respiratory papillae. G: Unnumbered section posterior to F through the accessory copulatory spicules (dissolved) of the mantle, bump indicated by arrowhead (cf. Figure 3C). Key: 1, upper gametoduct; 2, lower gametoduct; AS, accessory copulatory spicule; AU, auricle; CS, copulatory spicule/spicule pocket; GP, gametopore; MC, mantle cavity; MG, midgut gland; OV, ovum; PC, pericardial cavity; R, rectum; SC, suprarectal commissure; SR, seminal receptacle; V, ventricle. Scale bars: A-C, E, F = 0.1 mm; D, G = 0.05 mm.

Chaetoderma argenteum Heath, a Northeastern Pacific Aplacophoran Mollusk Redescribed (Chaetodermomorpha: Chaetodermatidae)

by

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Abstract. *Chaetoderma argenteum* Heath, 1911, has been collected in the northeast Pacific from Point Conception, California, to southeast Alaska between 70 and 600 m. Synonyms are *C. attenuata* Heath, 1911, and *C. montereyensis* Heath, 1911. Since 1960, several surveys have taken *C. argenteum* from the Santa Maria Basin, from off the Oregon coast, and from both offshore and inshore waters of southwest British Columbia in numbers large enough to provide material for experimental research.

Chaetoderma argenteum is redescribed and illustrated. It is distinguished from all other *Chaetoderma* species of the east Pacific by the anterior trunk spicules, which are bent and thickened on each side of an abfrontal groove, and by the large radula cone, which is curved in lateral view.

INTRODUCTION

Chaetoderma argenteum Heath, 1911, can predictably be collected from off southwestern Vancouver Island, British Columbia, from fine silt sediments, between 100 and 200 m. Specimens from this locality provided material for the first published account of spermiogenesis in a chaetoderm aplacophoran (BUCKLAND-NICKS & CHIA, 1989). The species has also recently been collected from inshore waters of British Columbia, from off the Oregon coast, and from the Santa Maria Basin off southern California. It thus appears to occur in large enough numbers at specific localities to provide material for fine structural analysis of anatomy and larval development, both of which are poorly studied in this group.

HEATH's (1911) original descriptions are not adequate for accurate species identification; he even mistook different sizes of *Chaetoderma argenteum* for different species.

Therefore this species is redescribed by external anatomy and morphology of hard parts using the criteria of SCHELTEMA (1976, 1989).

MATERIALS AND METHODS

Two hundred eleven specimens have been examined: 13 certain holotype and paratype specimens and 26 presumed paratypes collected between 1903 and 1904 by the U.S. Fisheries steamer *Albatross* (Table 1) and 172 recently collected specimens (Table 2). Most of the recently collected specimens were fixed as part of entire quantitative grab samples and sorted post-fixation. The fixatives used were not known to the authors; preservation was in buffered alcohol. Specimens used for scanning electron microscopy (SEM) were sorted alive, dissected, and then fixed in 2% glutaraldehyde buffered with 0.2 M sodium cac-

Table 1
Chaetoderma argenteum Heath, 1911, extant type material re-examined.

Albatross ¹ station	Locality	Depth (m)	Date (day/mo/yr)	No. specimens		Source ²
				Listed by Heath	Extant	
4231	Naha Bay, SE Alaska	148–203	7/VII/03	1	1, slides ³	CAS
4244	Kasaan Bay, SE Alaska	90–97	11/VII/03	1	—	—
4244, 4250	Samples mixed	—	—	—	3	MCZ
4250	off Stikine R., SE Alaska	110–119	13/VII/03	5	1	MCZ
					1, slides ³	CAS
4252	Stephens Passage, SE Alaska	356–362	14/VII/03	2	2	MCZ
4485	Monterey Bay	70–194	17/V/04	9	—	—
4508	Monterey Bay	526–640	20/V/04	7	—	—
4510 ⁴	Monterey Bay	164–331	?/V/04	—	19	MCZ
4522	Monterey Bay	234–268	26/V/04	139	1	MCZ
4523	Monterey Bay	135–194	26/V/04		1	MCZ
4524	Monterey Bay	383–410	26/V/04		2	MCZ
4525	Monterey Bay	400	26/V/04		—	—
4526 ⁴	Monterey Bay	367	26/V/04	—	7	MCZ
n.d.	Monterey Bay	n.d.	n.d.	1	1, slides ³	CAS

¹ From U.S. COMMISSION OF FISH AND FISHERIES (1905) and U.S. BUREAU OF FISHERIES (1906).

² CAS = California Academy of Sciences; MCZ = Museum of Comparative Zoology (Harvard University).

³ Holotypes.

⁴ Not listed by HEATH (1911) but specimens were presumably examined by him and are considered to be paratypes.

dylate buffer (pH 7.4) at 4°C for 2 h. Following a rinse in the same buffer, tissues were post-fixed in 1% osmium tetroxide in the same buffer at 4°C for 1 h. The tissues were dehydrated in an ethanol series, exchanged in incremental steps through amyl acetate, and critical point dried. Selected body parts were mounted on SEM stubs, sputter coated with gold, and examined in a Cambridge S250 stereoscan scanning electron microscope.

Spicules used for camera lucida drawings were removed from alcohol-preserved specimens with a fine needle and transferred by pipette into glycerine; or the specimen was placed directly into glycerine before removing the spicules. For SEM, segments of specific areas of the body were isolated and treated with 2% sodium hypochlorite (household bleach) until the tissues were dissolved. Spicules were removed from the dish with a Pasteur pipette, passed

through three rinses of distilled water, transferred into ethanol, and then air dried on SEM stubs. The spicules were sputter coated with gold prior to examination. Radulae for camera lucida drawings were dissected by making a dorsal longitudinal slit in the head region, removing the entire buccal mass, and dissolving the tissue in hypochlorite solution. The radulae were washed thoroughly and placed in glycerine for drawing. Preparation of radulae for SEM was similar to that for spicules.

Body measurements of entire preserved specimens were made from camera lucida drawings with dividers or a map-measuring wheel, and of sectioned type material with scale bars drawn on camera lucida drawings.

Type material is at the California Academy of Sciences (CAS) and Museum of Comparative Zoology (Harvard University) (MCZ).

Table 2
Chaetoderma argenteum Heath examined from recent collections.

Locality	Depth (m)	No. specimens	Source ¹
Off SW Vancouver Is., BC	100–200	96	SEATECH-IOS; Buckland-Nicks
Alice Arm, Hastings Arm, of Observatory Inlet, BC	400–600	36	IOS
Saanich Inlet, BC	90	4 ²	D. A. Bright, Univ. Victoria
Off Oregon coast	150–200	11	OSU
Santa Maria Basin	113–410	25 ²	MMS; Santa Barbara Museum

¹ SEATECH-IOS = Canadian Government Survey, Institute of Ocean Sciences, Sidney, BC; OSU = Oregon State University; MMS = Minerals Management Service, U.S. Department of Interior.

² Voucher specimens only.

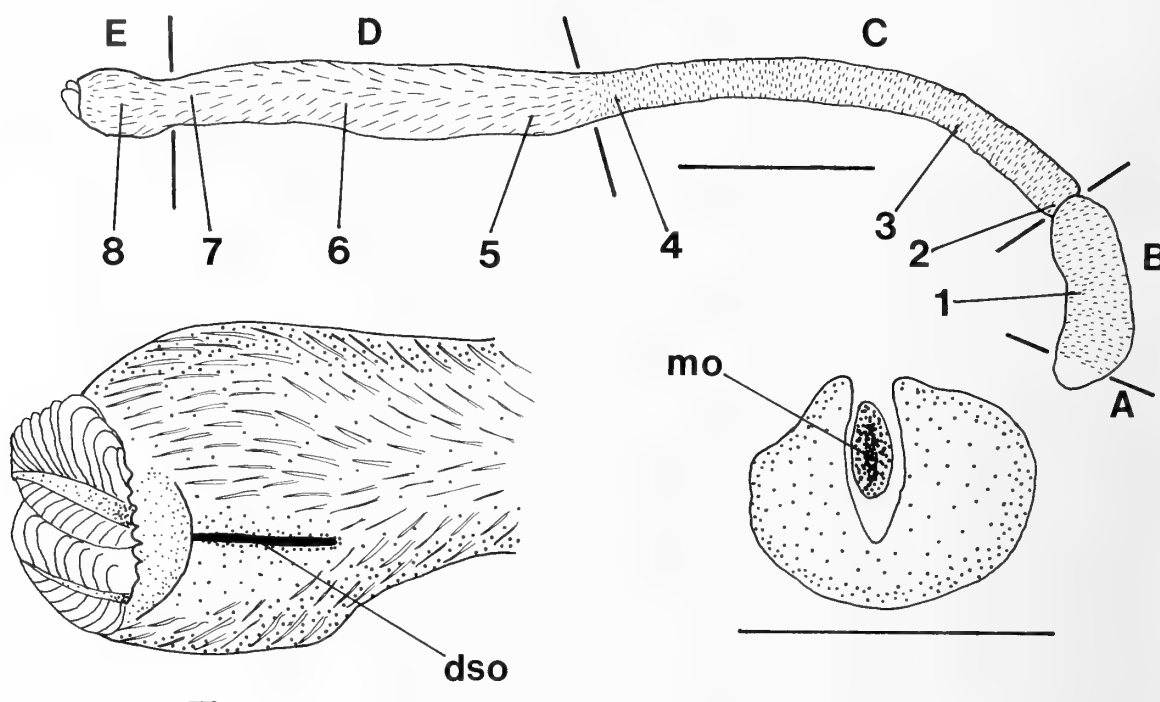


Figure 1

Chaetoderma argenteum Heath. *Chaetoderma montereyensis* Heath paratype (Albatross stn. 4524) (MCZ). Above, entire specimen showing body regions: A, anterior; B, neck; C, anterior trunk; D, posterior trunk; E, posterior; and positions 1-8 from which spicules were drawn (see Figure 3); scale bar = 5.0 mm. Lower left, posteriorm showing extended ctenidia (cf. Figure 2C) and dorsoterminal sense organ (dso); lower right, oral shield with dorsal cleft around mouth opening (mo) (cf. Figure 2D). Lower left and right, same paratype as above; scale bars = 1.0 mm.

SYSTEMATICS

Subclass Chaetodermomorpha Pelseneer, 1906

Caudofoveata Boettger, 1956

Aplacophoran mollusks without a foot or ventral groove; with a cuticular oral shield and paired ctenidia in the mantle cavity; stomach and digestive gland separate; dioecious.

Family CHAETODERMATIDAE Marion, 1885

Oral shield unpaired; radula with a cone-shaped cuticular piece (=peg, tongue) and a single pair of denticles; body with four distinct regions reflecting internal anatomy.

Chaetoderma Lovén, 1844

Crystallophrisson Möbius, 1875. IVANOV, 1981 (see SALVINI-PLAWEN, 1984).

Type species: *Chaetoderma nitidulum* Lovén, 1844, by monotypy.

Radula with paired denticles lying outside dome-shaped cuticular membrane that covers buccal mass and with paired lateral projections extending from radula cone to dome-

shaped membrane beneath base of denticles (see SCHELEMA, 1972).

Range: Worldwide from 8 to 2260 m.

Chaetoderma argenteum Heath, 1911

Chaetoderma argentea HEATH, 1911:43, 62-63, pl. 4 fig. 7, pl. 26 figs. 1-7, pl. 36 fig. 1, pl. 37 fig. 6 (SE Alaska, Behm Canal, near Naha Bay, 148-203 m; Albatross stn. 4231, 7/VII/03. **Type:** Holotype as serial sections and spicules, CAS 021392. Described from single specimen.

Chaetoderma attenuata HEATH, 1911:43, 55-59, pl. 4 figs. 3, 10, pl. 5 fig. 1, pl. 12 fig. 4, pl. 25 figs. 1-10 [figs. 1-3, 6, 7 of type], pl. 36 fig. 2, pl. 37 fig. 8 (SE Alaska, Stikine River delta, 110-119 m; Albatross stn. 4250, 13/VII/03). **Types:** Holotype as serial sections and spicules, CAS 021393; paratypes as 6 wet specimens, MCZ.

Chaetoderma montereyensis HEATH, 1911:43, 61-62, pl. 4 figs. 4, 8, 14, 17, pl. 27 figs. 1, 2, 4-11 [figs. 2, 5, 7-9 of type], pl. 37 figs. 2, 3 (Monterey Bay, California) (no Albatross stn. no.). **Types:** Holotype as serial sections, no spicule slide, CAS 021397; 4 certain and 26 probable paratypes as wet specimens, MCZ.

?*Crystallophrisson kajanovi* IVANOV, 1984. [Caudofoveata (Mollusca, Caudofoveata) in Peter the Great Bay (Sea of Japan)] pp. 36-37, fig. 4. [In Russian.]

Chaetoderma sp. BUCKLAND-NICKS & CHIA, 1989:308-317, figs. 1-22.

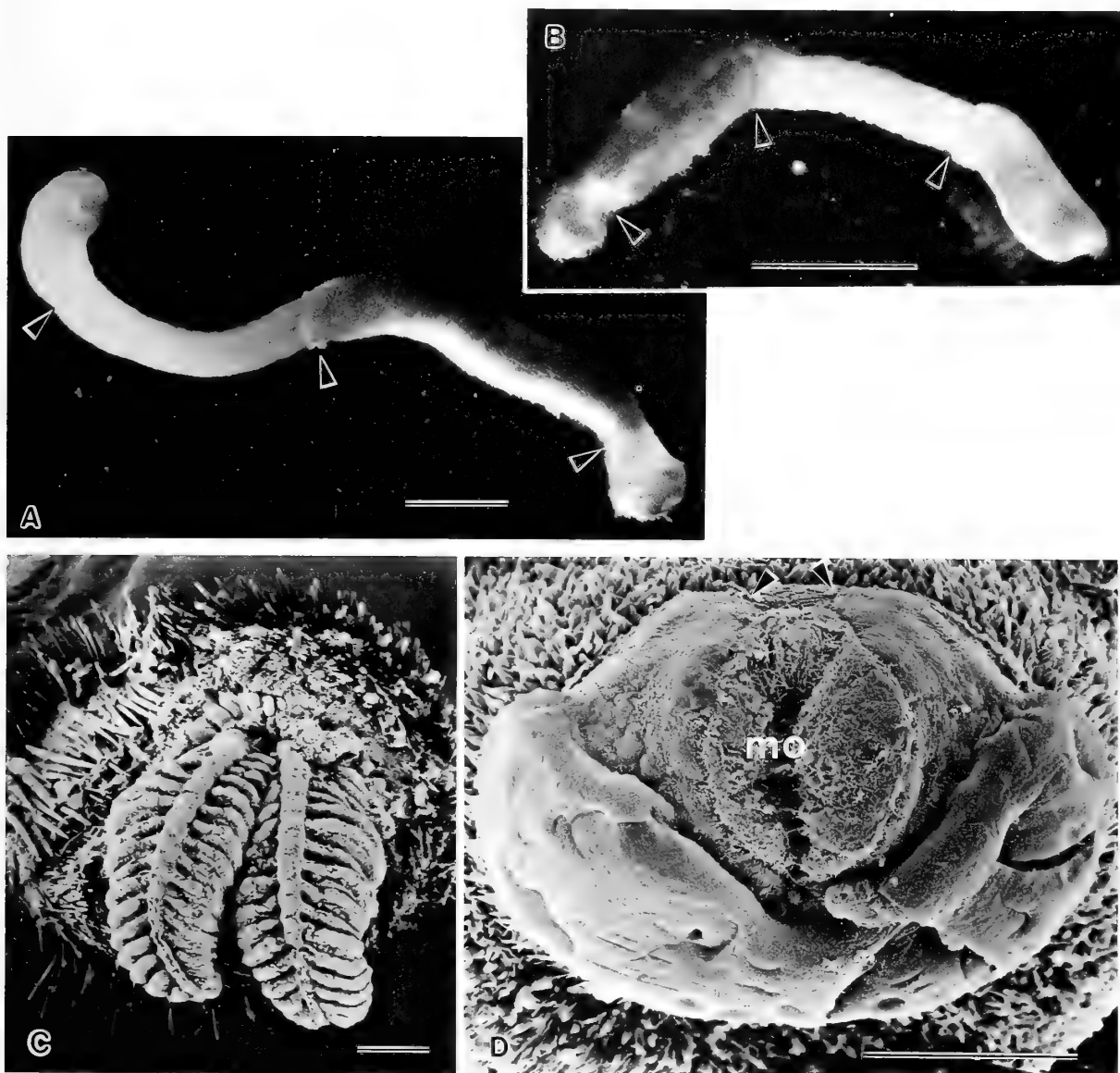


Figure 2

Chaetoderma argenteum Heath from 110 m adjacent to Rainy Bay, Vancouver Island, BC. A, B: Living specimens showing change in shape caused by muscle contraction and hydrostatic expansion. Arrowheads indicate boundaries between body regions (cf. Figure 1). C: Ctenidia extended from mantle cavity, scanning electron photomicrograph (SEM); long axes indicate dorsally situated efferent channels, and ctenial leaves are alternate. D: Oral shield with open mouth (mo); arrowheads indicate edge of cuticle at dorsal cleft. Note that ventral part of shield appears thicker than dorsal part around mouth. Scale bars: A, B = 3 mm, C, D = 200 μ m.

Range: Off Pt. Conception, California, to southeast Alaska, from 70 to 640 m; ?Sea of Japan, 33–69 m.

Diagnosis: Greatest length to more than 40 mm; anterior constriction pronounced; anterior trunk usually longer than posterior trunk and often narrower than neck; posterior trunk up to 2.0 mm in diameter. Oral shield with dorsal cleft. Spicules erect on anterior trunk and flat against posterior trunk. Spicules widest at base, those of anterior trunk bent, thickened on each side of base forming abfrontal

groove, up to 130 μ m long, those of posterior trunk pyramidal, flat, keeled, with two or more sharp lateral ridges, up to 263 μ m; radula cone large, up to 510 μ m long, curved, wider laterally than frontally, lateral projections up to 250 μ m long.

DESCRIPTION

Body: Preserved, contracted specimens of *Chaetoderma argenteum* typically have an anterior trunk (region C) either

Table 3

Body measurements and ratios of specimens belonging to Heath types of *Chaetoderma argenteum*, *C. attenuata*, and *C. montereyensis*.

Species	Measurements (mm)											
	Body length			Neck (B) diam. ¹			Ant. trunk (C) diam. ¹			Post. trunk (D) diam. ¹		
	<i>ar.</i>	<i>at.</i>	<i>m.</i>	<i>ar.</i>	<i>at.</i>	<i>m.</i>	<i>ar.</i>	<i>at.</i>	<i>m.</i>	<i>ar.</i>	<i>at.</i>	<i>m.</i>
Heath, 1911 ²	24	45, 61	45	—	—	—	1.6	1.5, 1.7	2	2.6	2.6, 2.7	3
Type slides	—	—	—	1.2	—	—	0.8	0.5	1.3	1.1	0.8	1.4
Paratypes ³	—	39–42	14–34	—	1.0–1.6	0.8–1.5	—	0.8–1.2	0.8–1.4	—	1.1–1.9	0.8–2.0

	Ratios								
	B/C diam.			C/D length			C/D diam.		
	<i>ar.</i>	<i>at.</i>	<i>m.</i>	<i>ar.</i>	<i>at.</i>	<i>m.</i>	<i>ar.</i>	<i>at.</i>	<i>m.</i>
Computed from Heath, 1911	—	—	—	—	—	—	0.62	0.65	0.67
Type slides	—	1.50	—	1.46 ⁴	—	—	0.72	0.62	0.93
Paratypes ³ (mean)	—	1.26	1.05	—	1.45	1.10	—	0.64	0.80

¹ See Figure 1 for body regions.

² Heath does not state whether these are measurements of alive or fixed animals.

³ For *C. montereyensis*, all *Albatross* specimens are considered to be paratypes.

⁴ Determined from pl. 4, fig. 7 (HEATH, 1911).

equal in diameter to or narrower than the neck (region B) and longer than the posterior trunk (region D) (Figure 1, Table 3). In living specimens the relative lengths of the two trunk regions change, reflecting movements under hydrostatic control (cf. Figure 2A, B). The erect spicules of the neck and anterior trunk are dense; the flat-lying spicules of the posterior trunk are more sparse. The oral shield is cleft dorsally (Figures 1, 2), a morphology that was recognized by HEATH (1911) in *C. attenuata*, but that he illustrated incorrectly in *C. montereyensis* as being pierced by the mouth opening (HEATH, 1911:pl. 4, figs. 14, 17). Posteriorly the dorsoterminal sense organ is obvious and about 1 mm in length in large specimens. The spicules of the posterium do not form a terminal ring.

Spicules: Spicules from all body regions are widest basally and range up to more than 10 μm in thickness. Neck spicules (no. 1, Figures 3, 5) are mostly narrow, thickest medially at the flared base, and curved in lateral view; they are less than 100 μm long and up to 25 μm wide. Spicules from the anterior trunk are longest near the anterior constriction (no. 2), up to 130 μm in length, decreasing to 90 μm at the midpoint (no. 3) and to 80 μm next to the posterior trunk (no. 4). All are thickened on each side abfrontally producing a groove (Figures 3, isochromes; 5E) and all are bent and flared basally, ranging up to 40 μm wide. Spicules near the posterior trunk bear a sharp keel (no. 4). Spicules on the posterior trunk region change abruptly; they are flat, sharply keeled with one or more sharp or rounded lateral ridges on each side, and gradually tapered from the broad base (nos. 5–7). Length increases from a maximum of 170 μm anteriorly to 265 μm posteriorly and greatest width at the base increases

from 50 to 60 μm . Thickness exceeds 10 μm only medially on the keel. There are numerous fine axial striations on the base (Figure 5C). Spicules of the posterium are without a keel, more than 400 μm long, 40 μm or more wide, and thickest medially (no. 8).

Radula: The cone-shaped piece is large, up to 510 μm long, 140 μm wide in frontal view, and 190 μm wide in lateral view (Figures 4, 5); in lateral view it curves and tapers to a narrow end. The lateral projections are broad and up to 250 μm long. Denticles are rather small, between 30 and 60 μm long. The cuticular dome extends proximally one-half the length of the cone. (Measurements based on five isolated radulae.)

REMARKS

Heath considered *Chaetoderma argenteum* of different sizes or from geographically separated populations as distinct species, although he did not differentiate *C. argenteum*, *C. attenuata*, and *C. montereyensis* either by written description or by illustration. STORK (1941) already noted the similarity between *C. attenuata* and *C. montereyensis* in Heath's descriptions. In several characters examined here in types and newly collected specimens, no differences at a species level were detected among the three *Chaetoderma* species described by Heath. Precedence is given to the name *C. argenteum* because of its page position (HEATH, 1911: 43).

The lengths and diameters of body regions and their ratios are shown in Table 3 for Heath's types and paratypes. Although total body length as published by Heath and measured on types is seen to differ among his species,

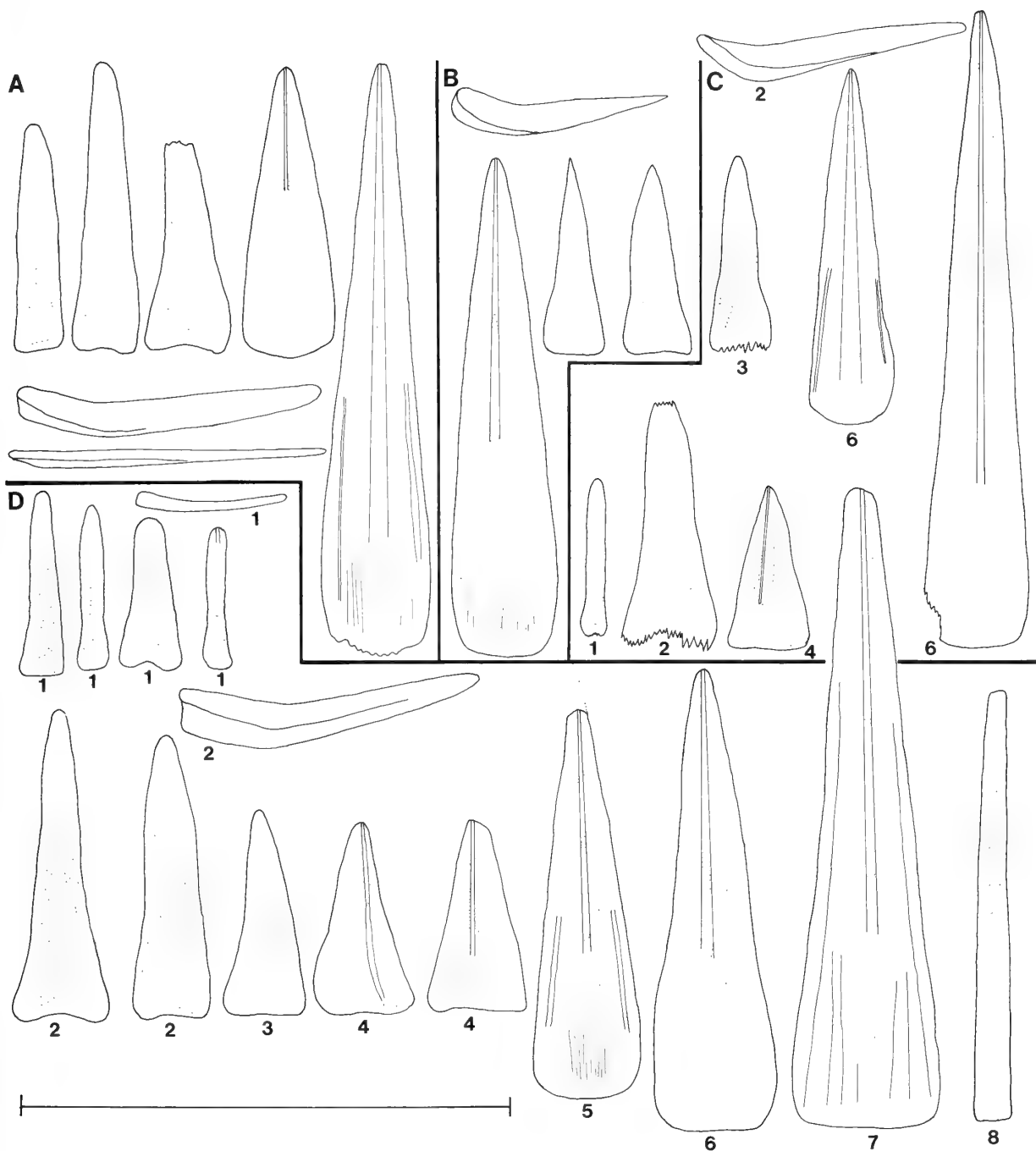


Figure 3

Spicules of *Chaetoderma argenteum* Heath. Lateral views with long axis horizontal; isochromes (lines of equal thickness as seen under cross-polarized light) indicated by dotted lines. A: Holotype spicules, *C. argenteum*, CAS 021392. B: Holotype spicules, *C. attenuata* Heath, CAS 021393. C: Paratype spicules, *C. attenuata* (Albatross stn. 4252, MCZ); numbers refer to body positions indicated in Figure 1. D: Paratype spicules, *C. montereyensis*, from specimen drawn in Figure 1 showing positions 1–8 from which spicules were drawn. Scale bar = 200 μm , except for spicule D8 = 500 μm .

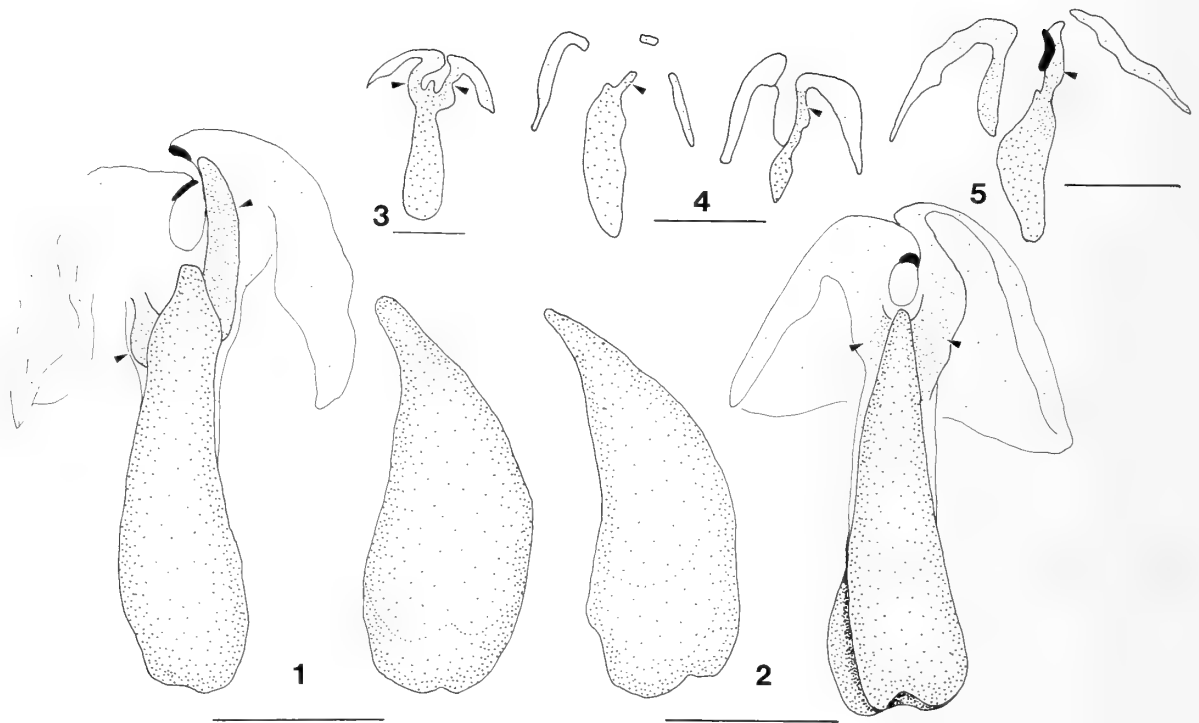


Figure 4

Radula of *Chaetoderma argenteum* Heath (cf. Figure 5C, D). 1: Frontal and lateral views of *C. attenuata* Heath paratype (MCZ) (*Albatross* stn. 4252). 2: Lateral and frontal views of *C. montereyensis* Heath, specimen presumed part of type series (MCZ) (*Albatross* stn. 4510). 3: Section of *C. attenuata* Heath holotype (CAS 021393). 4: Two sections of *C. argenteum* Heath holotype (CAS 021392). 5: Section of *C. montereyensis* Heath holotype (CAS 021397). Arrowheads indicate lateral projections. Scale bars = 200 μ m.

measured diameters of the neck (region B), anterior trunk (region C), and posterior trunk (region D) fall within the same ranges (0.8–1.6 mm, 0.5–1.4 mm, and 0.8–2.0 mm, respectively). The ratios of neck to anterior trunk diameters, anterior to posterior trunk diameters, and anterior to posterior trunk lengths are also similar. In particular, the neck is usually wider than the anterior trunk (ratios 1.50, 1.26, and 1.05 for Heath's three species) and the anterior trunk is longer on average than the posterior trunk (ratios 1.46, 1.45, and 1.10).

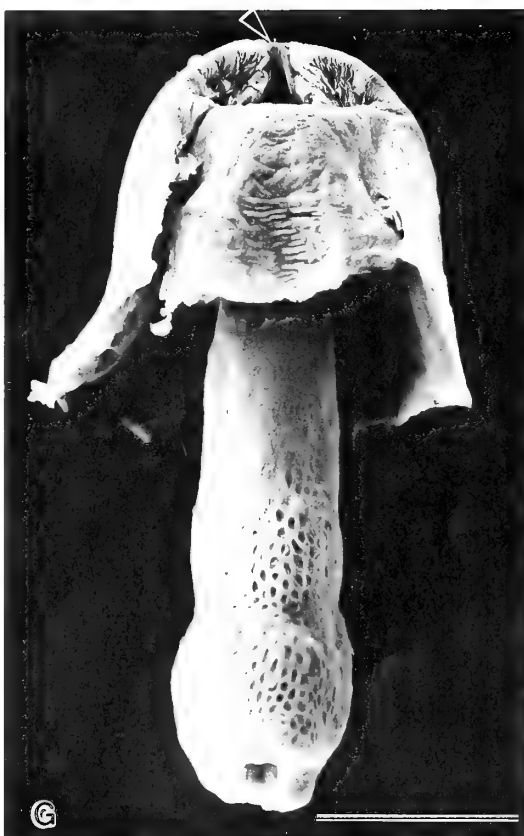
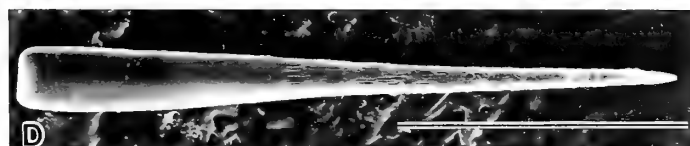
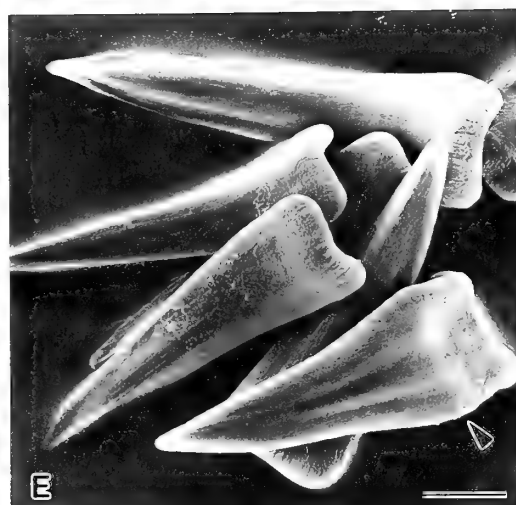
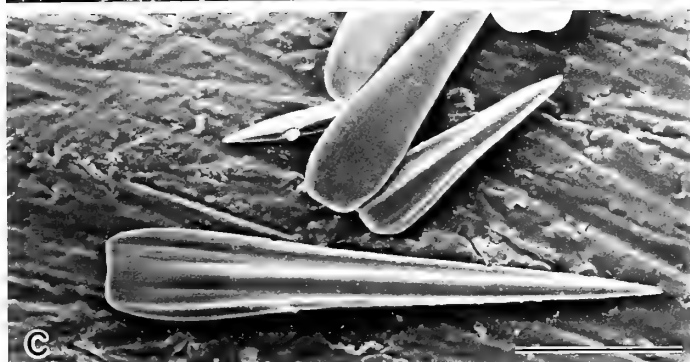
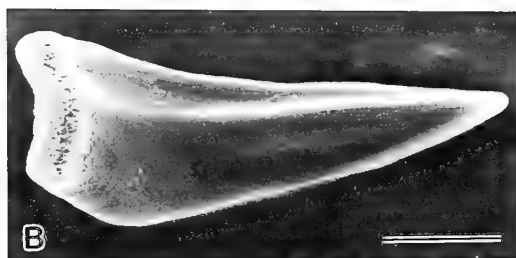
The oral shield is unknown for the single specimen of *Chaetoderma argenteum* described by Heath, but shields of paratypes of *C. attenuata* and *C. montereyensis* do not differ either in size or in being dorsally cleft, despite HEATH's

qualitative judgments of differences in relative size (1911: 43) or incorrect illustrations (1911: pl. 4, figs. 14, 17).

Heath fortunately made permanent spicule slides from the holotypes of *Chaetoderma argenteum* and *C. attenuata*. Paratypes of *C. montereyensis* and *C. attenuata* remained in good condition after nearly 90 years in alcohol and provided spicules from discrete body regions (Figures 1, 3). All of Heath's species have the diagnostic short, bent spicules with a broadly flared base and lateral abfrontal thickenings. These spicules are carried erect on the anterior trunk of *C. attenuata* and *C. montereyensis* paratypes. The same spicule attitude is indicated in the sections of the *C. argenteum* holotype, where the arrangement of spaces left by dissolved spicules in the cuticle of the anterior trunk

Figure 5

Chaetoderma argenteum Heath: spicules (A–E, scanning electron micrographs, cf. Figure 3) and radulae (F, light microscope, G, SEM, cf. Figure 4) from specimens recently collected off Rainy Bay, BC. A: From neck region. B, E: From anterior trunk; arrowhead on E indicates abfrontal view of broad lateral ridges and groove. C: From posterior trunk. D: From posteroventer. F: Frontal view, lateral projections (double arrowhead) and denticles (single arrowhead) seen in transmitted light. Note that cone becomes progressively tapered distally. G: Dome-shaped cuticular hood covering buccal mass as seen with SEM; denticles (arrowhead) lie outside of cuticular dome. Scale bars: A, B, E = 20 μ m; C, D, F, G = 100 μ m.



are the same as the spicule spaces in *C. attenuata* and *C. montereyensis* holotype sections from the same body region. The morphology of spicules from the anterior trunk separates *C. argenteum* from all other eastern Pacific *Chaetoderma* species.

The radulae from paratypes of *Chaetoderma attenuata* and *C. montereyensis* are morphologically indistinguishable. The cone is wide and curved in lateral view and the lateral projections are long and broad (Figure 4). The radula is broken in the holotype sections of *C. argenteum*, but size of the radula in relation to section diameter and size of the lateral projections are similar to those in holotype sections of *C. attenuata* and *C. montereyensis* (Figure 4, radulae 3, 4, 5).

A comparison of HEATH's (1911) written descriptions and examination of type sections of *Chaetoderma argenteum*, *C. attenuata*, and *C. montereyensis* offer no specific differences. Finally, new collections of Aplacophora from areas close to the type localities of *C. argenteum* and *C. attenuata* contain only a single species with bent, laterally thickened anterior trunk spicules. Therefore, we can conclude with a high degree of certainty that the synonymy is justified.

GEOGRAPHIC DISTRIBUTION

Including *Chaetoderma argenteum* and its synonyms, HEATH (1911) named eight northeast Pacific *Chaetoderma* species from Albatross collections. SCHWABL (1963) added nine further species from southern California collected during the Pacific Expedition of the Allan Hancock Foundation. Examination of Schwabl and Heath types indicates a reduction of these species by synonymy to perhaps 10 species, including *C. argenteum*. The number of *Chaetoderma* species known worldwide is about 37 to date; thus, approximately one-quarter of known species occurs in the northeast Pacific. The genus ranges in depth from 8 to 2260 m, but only a few species are restricted to depths less than 100 m or extend to more than 1000 m. The northeast Pacific species fit this depth pattern and are thus members of the upper continental slope fauna.

Chaetoderma argenteum has an amphi-Pacific distribution if *Crystallophrisson kafanovi* Ivanov (= *Chaetoderma kafanovi*) from the Sea of Japan is a synonym. There is at least one other probable amphi-oceanic *Chaetoderma* species. In the northern Atlantic, *C. nitidulum*, known as *C. nitidulum canadense* Nierstrasz in the western Atlantic (SCHELTEMA, 1973) (but considered a distinct species by SALVINI-PLAWEN, 1978), seems to occur on both sides of the ocean.

In 1904 numerous specimens of *Chaetoderma argenteum* were taken by the Albatross in Monterey Bay (Table 1), but since then it has been replaced by another unidentified species probably related to a form found south of Pt. Conception. However, *C. argenteum* has recently been collected south of Monterey Bay in the Santa Maria Basin from 113 to 410 m (Table 2).

ENVIRONMENT

In two studies of the effects of mine tailings on density and distribution of the invertebrate fauna in the inner reaches of Observatory Inlet, British Columbia (KATHMAN *et al.*, 1983, 1984), *Chaetoderma argenteum* was too scarce to be used as an indicator species. The study did show that the species was most abundant (50 m⁻²) in sediments of fine silt and clay near the sill at depths between 400 and 600 m, an area physically, chemically, and biologically different from the inner reaches. Adjacent to Rainy Bay, near Bamfield, Vancouver Island, British Columbia, *Chaetoderma argenteum* has repeatedly been found in similar fine silts at 110 m. It seems that the most likely sites for finding *C. argenteum* are the fjords and inlets of Canada and southeast Alaska in silty muds at depths greater than 100 m.

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Contribution no. 7512 of the Woods Hole Oceanographic Institution.

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Mollusca of Assateague Island, Maryland and Virginia: A Reexamination after Seventy-Five Years

by

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Abstract. A comparison was undertaken of molluscan collections in waters surrounding Assateague Island by J. Henderson and P. Bartsch in 1913 and collections by the present authors during 1988-1989. In 1914, Henderson and Bartsch reported 38 species of bivalves and 44 species of gastropods as compared with 33 species of bivalves and 40 species of gastropods in the present study. Of 82 species reported by Henderson and Bartsch, 50 are now present in Assateague waters plus an additional 25 species, including one species of Polyplacophora, and the cephalopod *Loligo pealeii*, that were not reported in their study. Of 11 gastropod taxa erected by Henderson and Bartsch for specimens collected in Chincoteague Bay, two species have been synonymized and the remaining nine species were not found in the present study. Stabilization of an inlet with a stone jetty after the hurricane of 1933 produced a salinity change in the bays of Assateague Island that may be responsible for some changes observed in the molluscan fauna.

INTRODUCTION

Studies of the Mollusca of the waters surrounding Assateague Island, Maryland and Virginia, have ranged from simple species lists (CARSON, 1945; BENNET, 1969) to reports on biology (SIELING, 1955b; WELLS, 1957; BOYNTON, 1970), diseases (SIELING, 1952; TAYLOR, 1958) and pests and their control (SIELING, 1955a, c, 1956, 1960; GRIFFITH & CASTAGNA, 1962). Although mollusks of the area have been detailed in general identification guides to the Atlantic fauna (MORRIS, 1973; ABBOTT, 1974, 1986; EMERSON & JACOBSON, 1976; REHDER, 1981), the only critical list of mollusks from these waters was produced by HENDERSON & BARTSCH (1914).

HENDERSON & BARTSCH (1914) reported 38 species of bivalves and 44 species of gastropods from Chincoteague Island, Virginia, from collections made during a week in the summer of 1913 in either Chincoteague Bay or the Atlantic waters just offshore. Eleven of the gastropods reported in their study were described as new species. Since their field study and report, the hydrography of waters surrounding Assateague Island has changed. This change is the result of the opening of Ocean City Inlet during the hurricane of 1933, and its subsequent stabilization by the U.S. Army Corps of Engineers (DOLAN *et al.*, 1977). This event changed a positive estuary, at the time of Henderson

and Bartsch's collections, extending from Assawoman Bay to Chincoteague Bay, into a reverse estuary now emptying at both Chincoteague Bay and Ocean City Inlet. That event had a significant impact on salinity and circulation in the bays behind Assateague Island. The present study was undertaken to determine changes in the molluscan fauna of waters surrounding Assateague Island, Maryland and Virginia, 75 years after the study of HENDERSON & BARTSCH (1914).

METHODS

The Study Site

Assateague Island is a barrier island system approximately 58 km in length and averaging 0.8 km in width (BIGGS, 1970) (Figure 1). The island is bounded on the north by Ocean City Inlet and on the south by Chincoteague Inlet, on the east by the Atlantic Ocean and on the west by the northern Sinepuxent Bay and southern Chincoteague Bay. The average depth of Sinepuxent Bay ranges from 1 to 1.5 m, with a 2-m channel, and deepens to 5-6 m at Ocean City Inlet. The maximum width of Chincoteague Bay is 11.6 km and the entire back bay system has an area of 428.9 km² (BIGGS, 1970). The depth of Chincoteague Bay ranges from 1 to 3 m, deepening to 28 m at

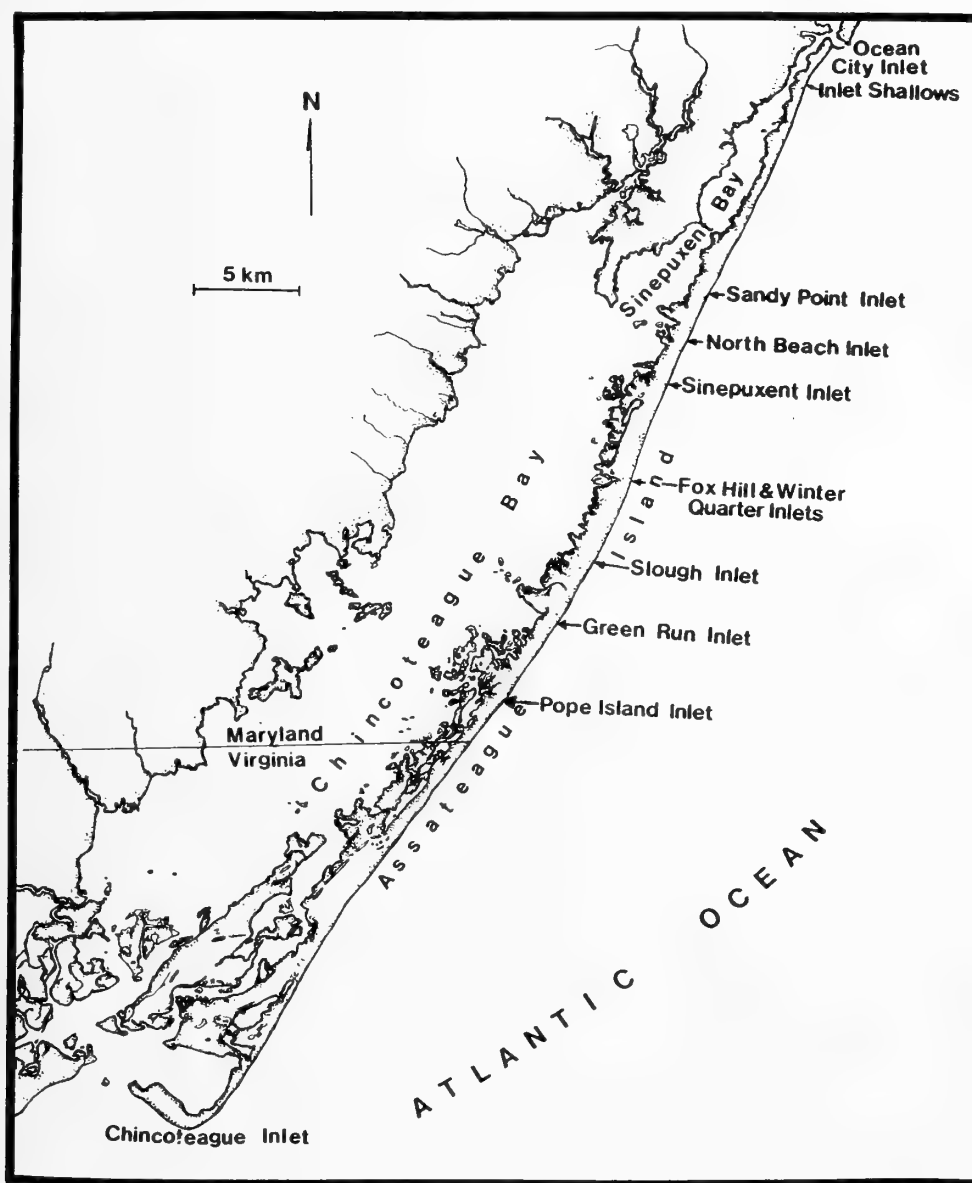


Figure 1

Assateague Island, Maryland and Virginia, showing general geography of the island and noting the locations of inlets cut through the island by storms (see Table 2).

Chincoteague Inlet. The southern end of the island contains Tom's Cove, formed by a westward bending sand spit (Fishing Point) and the main body of the island. The average depth of Tom's Cove is 1 m.

SELING (1954a) described the physical characteristics of the waters surrounding Assateague Island. In summer months, water temperatures are cooler at the inlets and warmer in the shallow bays. In the winter, this pattern is reversed and occasionally the bays will freeze over with ice. In summer, salinities decrease toward the inlets where tidal surge mixes seawater with high salinity bay water.

The salinity pattern reverses during the winter and spring months. Summer salinity patterns result from a net water loss from evaporation that is made up by tidal inflow and a minimal freshwater inflow from the freshwater streams of the mainland (PELLENBARG & BIGGS, 1970). Summer 1989 was characterized by higher than usual rainfall and salinities ranged from 27 to 29 ppt in Sinepuxent Bay and from 24 to 25 ppt in Chincoteague Bay, the highest salinities being measured near the inlets. Tidal amplitudes are not dramatic, being approximately 1 m at the inlets and 0.33 m in the bays. The currents of Chincoteague and

Table 1

Molluscan taxa found in waters surrounding Assateague Island during the present study and compared with that of HENDERSON & BARTSCH (1914) [+ = Present, - = Absent]. Two gastropod species described by HENDERSON & BARTSCH (1914) (*Cerithiopsis virginica* [= *Cerithiopsis greeni*] and *Epitonium virginicum* [= *Epitonium multistriatum*]) are not listed because of subsequent synonymy.

Taxa	Pre- sent study	Hender- son and Bartsch
Bivalvia		
<i>Abra aequalis</i> (Say, 1822)	-	+
<i>Anadara ovalis</i> (Bruguière, 1789)	+	+
<i>Anadara transversa</i> (Say, 1822)	+	+
<i>Anomia simplex</i> Orbigny, 1842	+	+
<i>Argopecten gibbus</i> (Linné, 1758)	+	+
<i>Argopecten irradians irradians</i> (Lamarck, 1819)	+	-
<i>Argopecten irradians</i> f. <i>concentricus</i> (Say, 1822)	+	-
<i>Astarte castanea</i> (Say, 1822)	+	+
<i>Barnea truncata</i> (Say, 1822)	+	-
<i>Chione cancellata</i> (Linné, 1767)	+	+
<i>Corbula contracta</i> Say, 1822	-	+
<i>Crassinella lunulata</i> (Conrad, 1834)	+	+
<i>Crassostrea virginica</i> (Gmelin, 1791)	+	+
<i>Cyclocardia borealis</i> (Conrad, 1831)	+	+
<i>Cyrtopleura costata</i> (Linné, 1758)	+	+
<i>Dinocardium robustum</i> (Lightfoot, 1786)	-	+
<i>Divaricella quadrisulcata</i> (Orbigny, 1842)	+	+
<i>Donax variabilis</i> Say, 1822	+	+
<i>Ensis directus</i> Conrad, 1843	+	-
<i>Ensis minor</i> Dall, 1900	-	+
<i>Gemma gemma</i> (Totten, 1834)	+	-
<i>Guekensia demissa</i> (Dillwyn, 1817)	+	-
<i>Ischadium recurvum</i> (Rafinesque, 1820)	+	-
<i>Laevicardium mortoni</i> (Conrad, 1830)	-	+
<i>Linga pennsylvanica</i> (Linné, 1758)	-	+
<i>Lyonsia hyalina</i> Conrad, 1831	-	+
<i>Macoma balthica</i> (Linné, 1758)	+	-
<i>Macoma tenta</i> (Say, 1834)	-	+
<i>Mercenaria mercenaria</i> (Linné, 1758)	+	+
<i>Mulinia lateralis</i> (Say, 1822)	+	+
<i>Mya arenaria</i> Linné, 1758	+	+
<i>Mytilus edulis</i> Linné, 1758	+	+
<i>Noetia ponderosa</i> (Say, 1822)	+	+
<i>Nucula proxima</i> Say, 1822	-	+
<i>Nuculana acuta</i> (Conrad, 1831)	-	+
<i>Petricola pholadiformis</i> (Lamarck, 1818)	+	+
<i>Pitar morrhuanus</i> (Linsley, 1848)	-	+
<i>Pleuromeris tridentata</i> (Say, 1826)	-	+
<i>Raeta plicatella</i> (Lamarck, 1818)	+	+
<i>Solemya velum</i> Say, 1822	+	-
<i>Solen viridis</i> Say, 1821	+	-
<i>Spisula solidissima</i> (Dillwyn, 1817)	+	+
<i>Spisula solidissima similis</i> (Say, 1822)	-	+
<i>Tagelus divinus</i> (Spengler, 1794)	-	+
<i>Tagelus plebeius</i> (Lightfoot, 1786)	+	+
<i>Tellina agilis</i> Stimpson, 1857	+	+
<i>Yoldia limatula</i> (Say, 1831)	-	+

Table 1

Continued

Taxa	Pre- sent study	Hender- son and Bartsch
Gastropoda		
<i>Acanthodoris pilosa</i> (Müller, 1776)	+	-
<i>Acteocina canaliculata</i> (Say, 1822)	+	+
<i>Anachis avara</i> (Say, 1822)	+	+
<i>Boonea impressa</i> (Say, 1821)	-	+
<i>Buccinum undatum</i> Linné, 1758	+	-
<i>Busycon canaliculatum</i> (Linné, 1758)	+	+
<i>Busycon carica</i> (Gmelin, 1791)	+	+
<i>Busycon sinestrum</i> (Hollister, 1958)	+	+
<i>Cerithiopsis greeni</i> (C. B. Adams, 1839)	-	+
<i>Clathurella jewetti</i> Stearns	-	+
<i>Cratena pilata</i> ('Gould' Binney, 1870)	+	-
<i>Crepidula convexa</i> Say, 1822	+	+
<i>Crepidula fornicata</i> (Linné, 1758)	+	+
<i>Crepidula plana</i> Say, 1822	+	+
<i>Creseis virgula</i> (Rang, 1828)	+	-
<i>Crucibulum striatum</i> Say, 1824	+	-
<i>Cylichnella bidentata</i> (Orbigny, 1841)	+	+
<i>Diastoma alternatum virginicum</i> Henderson & Bartsch, 1914	-	+
<i>Diodora cayenensis</i> (Lamarck, 1822)	+	+
<i>Epitonium angulatum</i> (Say, 1830)	+	-
<i>Epitonium humphreysi</i> (Kiener, 1838)	+	+
<i>Epitonium multistriatum</i> (Say, 1826)	+	+
<i>Epitonium rupicola</i> (Kurtz, 1860)	+	+
<i>Eupleura caudata</i> (Say, 1822)	+	+
<i>Ilyanassa obsoleta</i> (Say, 1822)	+	+
<i>Inodrillia dalli</i> (Verrill & Smith, 1882)	+	-
<i>Kurtziella cerina</i> (Kurtz & Stimpson, 1851)	+	+
<i>Littorina irrorata</i> (Say, 1822)	+	+
<i>Littorina littorea</i> (Linné, 1758)	+	-
<i>Littorina saxatilis</i> (Olivieri, 1792)	+	-
<i>Lunatia heros</i> (Say, 1822)	+	+
<i>Lunatia pallida</i> (Broderip & Sowerby, 1829)	-	+
<i>Lunatia triseriata</i> (Broderip & Sowerby, 1829)	+	-
<i>Mangilia</i> sp.	-	+
<i>Marginella roscida</i> Redfield, 1860	-	+
<i>Melampus bidentatus</i> Say, 1822	+	-
<i>Melanella intermedia</i> (Cantraine, 1835)	+	+
<i>Mitrella lunata</i> (Say, 1826)	+	+
<i>Nassarius trivittatus</i> (Say, 1826)	+	+
<i>Nassarius vibex</i> (Say, 1822)	+	+
<i>Odostomia pocahontasae</i> Henderson & Bartsch, 1914	-	+
<i>Odostomia toyotani</i> Henderson & Bartsch, 1914	-	+
<i>Odostomia virginica</i> Henderson & Bartsch, 1914	-	+
<i>Olivella mutica</i> (Say, 1822)	+	-
<i>Polinices duplicatus</i> (Say, 1822)	+	+
<i>Sinum perspectrum</i> (Say, 1831)	+	+
<i>Terebra concava</i> Say, 1827	-	+
<i>Terebra dislocata</i> (Say, 1822)	+	+
<i>Thais haemastoma</i> f. <i>floridana</i> (Conrad, 1837)	+	-

Table 1
Continued

Taxa	Pre- sent study	Hender- son and Bartsch
<i>Triphora nigrocincta</i> (C. B. Adams, 1839)	—	+
<i>Triphora pyrrrha</i> Henderson & Bartsch, 1914	—	+
<i>Turbonilla pocahontasae</i> Henderson & Bartsch, 1914	—	+
<i>Turbonilla powhatani</i> Henderson & Bartsch, 1914	—	+
<i>Turbonilla toyatani</i> Henderson & Bartsch, 1914	—	+
<i>Turbonilla virginica</i> Henderson & Bartsch, 1914	—	+
<i>Urosalpinx cinerea</i> (Say, 1822)	+	+
Cephalopoda		
<i>Loligo pealeii</i> Lesueur, 1821	+	—
Polyplacophora		
<i>Chaetopleura apicalata</i> (Say, 1830)	+	—

Sinepuxent bays are mostly independent of the non-tidal oceanic currents and water flows away from the inlets at Ocean City and at Chincoteague as the tides rise (PELLENBARG & BIGGS, 1970). Bay water circulation is such that the total water movement of the bays allows a daily water exchange of approximately 7.5% from outside sources (PRITCHARD, 1960). PELLENBARG & BIGGS (1970) report the bays to be essentially stagnant and intensely heated and stratified during summer months. SIELING (1954a) noted that currents throughout the bays, although of no great magnitude, may have some influence on shellfish larval distribution.

The Atlantic coastal waters of Assateague Island are shallow and PELLENBARG & BIGGS (1970) noted that they become rapidly stratified by mid-April and that there is little mixing between thermally stratified waters. Summer surface currents are generally onshore and the entire water mass has a northerly drift, perhaps due to the nearby Gulf Stream (PELLENBARG & BIGGS, 1970).

Mollusks are distributed over the North American Atlantic Coast in distinct provinces that are defined by the identity of the species found in a given area. One province is different from another when 50% of the species found in province A cannot be found in province B (PIELOU, 1979). Assateague Island is located in the Boreal Molluscan Province, which is characterized by low diversity and high population densities. The island is located just to the north (approximately 80 km) of the Virginian Subprovince (a subdivision of the Carolinian Province that includes the coast of Virginia to Florida and the Gulf states). Because the borders between provinces are not sharp, some faunal elements of the Virginian Subprovince are found in Assateague's waters or cast ashore as drift shells.

Collections

Molluscan collections were made monthly between April 1988 and August 1989. Collection methods included hand collecting, dredging, and bottom grab samples in all waters surrounding the island and at intertidal habitats such as the Ocean City Inlet jetty in the north and pier structures in the south. All materials collected were returned to the laboratory and identifications made using standard references to the Atlantic Coast fauna (MORRIS, 1973; ABBOTT, 1974, 1986; EMERSON & JACOBSON, 1976; REHDER, 1981). In those cases where taxonomic differences existed for a species, the taxonomy of ABBOTT (1974) was used. Additional records for the Chincoteague Bay area were provided by Dr. Robert S. Prezant, Indiana University of Pennsylvania, and Dr. Steve Rebach, University of Maryland Eastern Shore.

RESULTS

The present study revealed the presence of 75 species of Mollusca in the waters surrounding Assateague Island (Table 1). HENDERSON & BARTSCH (1914) reported 82 species of which 50 were found in the present study. Although this appears to represent a net decline in molluscan diversity, the present study revealed the presence of 25 species not reported by Henderson and Bartsch.

Thirty-eight species of bivalves were reported by HENDERSON & BARTSCH (1914) while 33 species were found during the present study (Table 1). Species reported by them but not found during the present study include *Abra aequalis*, *Corbula contracta*, *Dinocardium robustum* (although they note that this may have been a drift shell), *Ensis minor*, *Laevicardium mortoni*, *Linga pennsylvanica*, *Lyonsia hyalina*, *Macoma tenta*, *Nucula proxima*, *Nuculana acuta*, *Pitar morrhuanus*, *Pleuromeris tridentata*, *Spisula solidissima similis*, *Tagelus divisus*, and *Yoldia limatula*. Bivalves found during the present study but not reported by HENDERSON & BARTSCH (1914) include *Argopecten irradians irradians*, *Argopecten irradians forma concentricus*, *Barnea truncata*, *Ensis directus*, *Gemma gemma*, *Geukensia demissa*, *Ischadium recurvum*, *Macoma balthica*, *Solemya velum*, and *Solen viridis*.

HENDERSON & BARTSCH (1914) reported 44 species of gastropods from Assateague waters while the present study reveals the presence of 40 (Table 1). Species reported by Henderson and Bartsch but not found during the present study include *Boonea impressa*, *Cerithiopsis greeni*, *Clathrella jewetti*, *Diastoma alternatum virginicum*, *Lunatia pallida*, *Mangilla* sp., *Marginella roscida*, *Odostomia pocahontasae*, *Odostomia toyatani*, *Odostomia virginica*, *Terebra convaca*, *Triphora nigrocincta*, *Triphora pyrrrha*, *Turbonilla pocahontasae*, *Turbonilla powhatani*, *Turbonilla toyatani*, and *Turbonilla virginica*. Gastropod species found during the present study but not found by Henderson and Bartsch were *Acanthodoris pilosa*, *Buccinum undatum*, *Cratena pilata*, *Creseis virgula*, *Crucibulum striatum*, *Epitonium angulatum*, *Inodrillia dalli*, *Littorina littorea*, *Littorina saxatilis*,

Lunatia triseriata, *Melampus bidentatus*, *Olivella mutica*, and *Thais haemastoma floridana*. The present study also revealed the presence of the cephalopod *Loligo pealeii* and the polyplacophoran *Chaetopleura apiculata*. No mollusks from these classes were reported by HENDERSON & BARTSCH (1914).

DISCUSSION

The collection methods of HENDERSON & BARTSCH (1914) cannot be exactly duplicated because they were inadequately described. However, several factors may account for changes in the molluscan fauna at Assateague Island from 1913 to 1989. The simplest explanation is that molluscan species were overlooked during the original study by HENDERSON & BARTSCH (1914): because their collections were made over the course of a few days in July 1913, it is not unreasonable that some species escaped notice. This is especially so of the pteropod *Creseis virgula*, which ranges from 40°N to 40°S (ABBOTT, 1974). The pelagic nature of this mollusk is such that it has been collected at Assateague Island only once in the last five years. Although the squid *Loligo pealeii* is not pelagic, encounters during just a few days of collecting would be unlikely. The nudibranch *Acanthodoris pilosa* is found with the sponge *Clione caelata*. Small infaunal species such as *Gemma gemma* could easily be missed without the proper collecting equipment. We were unable to locate specimens of *Macoma tenta* or *Tagelus divisus* though these species were collected in the late 1960s (DROBECK *et al.*, 1970).

Some species now found are newly introduced into Assateague waters. *Thais haemastoma* forma *floridana* was not present in Chincoteague Bay at the time of Henderson and Bartsch's collections. This gastropod, an important predator of barnacles, oysters, mussels, and other bivalves, is usually found from North Carolina south to Florida, the Caribbean, and Brazil (ABBOTT, 1974). SIELING (1960) first reported this species in Chincoteague Bay and noted that it was probably imported with transplanted oysters. With the decline of oyster populations, it is now rare. The identification of scallop species has also been in flux since HENDERSON & BARTSCH (1914) made their collections. Nevertheless, *Argopecten irradians irradians* was not taken in Chincoteague Bay until 1960 and its distribution was directly correlated with the invasion of the grass *Zostera marina* (BOYNTON, 1970).

The two littorinids found during the present study, *Littorina littorea* and *Littorina saxatilis*, are also notable. CLARKE (1971) and ABBOTT (1974) reported the range of *L. littorea* as Labrador to Maryland. The species is found along the coasts of Delaware and Maryland only on rock jetties or wooden groins. There has been some debate as to whether this species was introduced into North American waters from Europe (CLARKE, 1971) but archaeological evidence from Indian and Norse sites in Canada indicates that the species has been in North America since the 13th century (CLARKE & ERSKINE, 1961; CLARKE, 1963, 1971; MEDCOF

et al., 1965) or as early as 1000 AD (CLARKE, 1971). It is believed the species was restricted to Canadian waters and was transported south by ships sometime in the 1840s to 1880s or that unusually high air-sea temperatures allowed natural penetration of southern waters in the 1870s (CLARKE, 1971). Its southward spread is believed to be limited by higher water temperatures, but the sandy beaches of the southern coastal states may be more limiting than water temperature.

Other factors possibly explaining observed faunal differences are changes in back bay circulation, and therefore also in salinity, that resulted from the opening of the Ocean City Inlet. Historically, Assateague Island was usually continuous with Fenwick Island, Delaware and Maryland (KRAFT *et al.*, 1973; DOLAN *et al.*, 1977; LEATHERMAN, 1988). However, several transient inlets have opened the back bays of Assateague Island to the Atlantic, and the positions of these inlets have been noted over the past 250 years (Figure 1, Table 2). The hurricane of 1933 resulted in the opening of the Ocean City Inlet, which was subsequently stabilized by a jetty constructed by the U.S. Army Corps of Engineers in 1935 (LEATHERMAN, 1988). Until this event, the back bay system behind Fenwick-Assateague was essentially a positive estuary emptying into Chincoteague Bay with waters of relatively low salinities. However, the stabilization of the Ocean City Inlet has resulted in a permanent alteration of back bay circulation.

Marine molluscan habitats can be defined by salinity flux, and while molluscs may survive a wide range of salinity concentrations, specific behavioral, reproductive, and physiological activities may be dependent upon a much narrower range (DODGSON, 1928; SCHLIEPER, 1953; VERNBERG *et al.*, 1963; BAYNE, 1965; CASTAGNA & CHANLEY, 1973). *Crassostrea virginica* provides a well studied example. The overall salinity tolerance of this bivalve has been variously reported as 0–42.5 ppt (INGLE & DAWSON, 1951) and 5–30 ppt (GALTISOFF, 1964). However, the absolute minimum for survival has been reported as 0.2–3.6 ppt (BUTLER, 1952) and 4–5 ppt (RYDER, 1885; ARNOLD, 1868a, b; BELDING, 1912; LOOSANOFF, 1932). The salinity range for optimal survival was reported as 14.1–22.2 ppt (MOORE, 1900) but others state salinities greater than 7.5 ppt are the minimum for normal survival (LOOSANOFF, 1952; CHANLEY, 1958). While these salinity ranges imply wide latitude for the survival of individual oysters, other studies indicate that a narrower salinity range must exist for successful completion of certain life-cycle stages and physiological activities. FINGERMAN (1959) reported normal ciliary activity at 5–35 ppt and VERNBERG *et al.* (1963) reported a decrease in ciliary activity at 4 ppt. This agrees with studies that found salinities must be greater than 5 ppt for normal feeding activity (LOOSANOFF, 1952). Normal growth has been reported from greater than 10 ppt (LOOSANOFF, 1952) to an optimum of greater than 20 ppt (MEDCOF & NEEDLER, 1941; MEDCOF, 1944) and CHANLEY (1958) found a range of 12.5–25 ppt as the optimum for growth of newly metamorphosed larvae. The

minimum salinity for gametogenesis has been reported as 6 ppt (BUTLER, 1952) and 7.5 ppt (LOOSANOFF, 1952). Egg cleavage and development have been reported within ranges of 7.5 to 40.1 ppt (AMEMIYA, 1926; DAVIS, 1958) with optima at 10–22.5 ppt (DAVIS, 1958) and 19.3–35 ppt (AMEMIYA, 1926). DAVIS (1958) also reported a 10 ppt minimum for metamorphosis while PRYTHERCH (1934) reported the range over which metamorphosis will occur as 5.6–32.2 ppt. AMEMIYA (1926) reported normal larval development to occur between 14 and 39 ppt with an optimum of 25–29 ppt. Thus, even though a mollusk is found in waters whose salinity is within the range for survival, the salinity may be outside the range for other vital functions that ensure survival of the population.

Before the opening of the Ocean City Inlet, salinity in Chincoteague Bay was low enough that *Crassostrea virginica* existed there essentially free of parasitic diseases and was not molested by such predators as *Eupleura caudata* or *Urosalpinx cinerea* (BOYNTON, 1970). SIELING (1961) reports that after stabilization of the inlet, oyster mortalities ranging from 50 to 100% occurred throughout Chincoteague Bay, with a high percentage of the affected oysters being infected by *Minchinia nelsoni* (MSX). Further, salinity concentrations above 15 ppt, while not directly affecting *C. virginica*, allowed optimum conditions for the survival of *E. caudata* and *U. cinerea* (DAIBER *et al.*, 1976).

Of the species now at Assateague Island but absent at the time of Henderson and Bartsch's collections, only the presence of *Ensis directus*, *Solemya velum*, and *Solen viridis* could be explained on the basis of higher salinities (CASTAGNA & CHANLEY, 1973). While salinity may be a prime factor in community composition change, its effects on individual species may not account for the species' survival at Assateague (DAVIES, 1972). Few of the species found by HENDERSON & BARTSCH (1914) should have experienced a fatal shift in salinity with the stabilization of the Ocean City Inlet (CASTAGNA & CHANLEY, 1973). While low salinities have been found in Chincoteague Bay since 1935 (SIELING, 1958), salinity is now, on the average, higher than in the period before stabilization of the Ocean City Inlet. However, the higher salinities of Chincoteague and Sinepuxent bays are still within the limits of tolerance for such species as *Ensis minor*, *Laevicardium mortoni*, *Lyonsia hyalina*, *Nucula proxima*, *Pleuromeris tridentata*, *Tagelus divisus*, and *Yoldia limulata* (CASTAGNA & CHANLEY, 1973). Further, no significant shift in bivalve feeding types has been observed. Using the bivalve feeding scheme of MORTON (1983), the proportions of suspension- and deposit-feeding bivalves have remained constant despite changes in species composition. The mollusks of Assateague have experienced population damage from hurricanes (SIELING, 1954b), invasions of several predators (SIELING, 1955a, b, 1960), and introductions of diseases (TAYLOR, 1958). The shift in molluscan community structure may be a combination of physiological effects of changes in hydrodynamics and salinity or changes in sediment composition (DAVIES, 1972).

Table 2

Location and dates of inlets of Assateague Island during the past 250 yr. See Figure 1 for locations. R = Recurring inlet. (After DOLAN *et al.*, 1977.)

Year(s)	Location
1700s	North Beach Inlet Sinepuxent Inlet (R) Green Run Inlet (R)
1766	Slough Inlet
1800s	Sinepuxent Inlet (R) Fox Hill Inlet Winter Quarter Inlet Green Run Inlet (R)
1841	North Beach Inlet (R)
1850s	Pope Island Inlet (R)
1870s	North Beach Inlet (R) Pope Island Inlet (R)
1900s	Sinepuxent Inlet (R)
1920	Sandy Point Inlet (R)
1933	Ocean City Inlet Inlet Shallows (R)
1962	Sandy Point Inlet (R)

Eleven species of gastropods have been described only from the waters of Chincoteague. These are *Cerithiopsis virginica*, *Diastoma virginica*, *Epitonium virginicum*, *Odostomia pocahontasae*, *Odostomia toyatani*, *Odostomia virginica*, *Triphora pyrrha*, *Turbonilla pocahontasae*, *Turbonilla powhatani*, *Turbonilla toyatani*, and *Turbonilla virginica*. All of these species were described by HENDERSON & BARTSCH (1914) from waters off Chincoteague Island, Virginia. Several of these species have since been synonymized. *Cerithiopsis virginica* and *Epitonium virginicum* are now recognized as junior synonyms of *Cerithiopsis greeni* and *Epitonium multistriatum*, respectively. *Triphora pyrrha* has been placed in the genus *Triphora* and is now recognized as *Triphora pyrrha*. *Diastoma virginica* is now recognized as a subspecies of *Diastoma alternatum* and is thus named *Diastoma alternatum virginicum*. Except for these synonymized taxa, none of the species described by HENDERSON & BARTSCH (1914) was found during our collections. Odostomids are sometime ectoparasites of oysters, mussels, and slipper shells and they feed by penetrating the tissues of the host animals and sucking their body fluids. Because of their restricted habitat, quasi-parasitic life cycle, and the decline of their principal host (oysters), they may in fact be extinct. They are not presently on the Federal List of Threatened and Endangered Species, but they are certainly candidates. However, before recommendation for protected status, a detailed survey of oyster and mussel beds should be conducted.

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Seasonal Changes in Outer Shell Layer Microstructure of *Mytilus edulis* in New Jersey, USA

by

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Abstract. In spring and fall, the outer shell layer of *Mytilus edulis* specimens collected from populations in New Jersey, USA, was composed of long, slender, evenly shaped prismatic needles deposited at angles of about 30° to the inner shell surface, where they terminated in distinct, chisel-shaped tips. (By definition, the long axis of a prism deposited at an angle of 0° was parallel to the inner shell surface and terminated at the posterior margin; angles increased in a clockwise direction.) Prisms deposited in summer were shorter, more uneven or lenticular in shape, and deposited at angles greater than 30°. Following growth interruptions in summer and winter, a cone-shaped region of such prisms was often formed in which prisms were deposited at angles as great as 140°. The inner surface of portions of the outer shell layer composed of these prisms often had a granular texture in which individual prism tips were indistinguishable. The outer layer microstructure of *M. edulis* could provide a record of the relative timing and severity of sublethal disturbances in specified time periods, creating an interpretative tool for ecological and paleoecological studies.

INTRODUCTION

The blue mussel *Mytilus edulis* Linné has three primary calcareous layers in its shell: an outer calcitic prismatic layer, an aragonitic myostracal layer to which the mantle is attached, and an inner aragonitic nacreous layer (TAYLOR *et al.*, 1969; CARRIKER, 1978). To date, investigations of seasonal changes in shell microstructure in the species have been limited to analyses of the inner nacreous layer. LUTZ (1976) found that the thickness of nacreous tablets decreased abruptly in spring in *M. edulis* from Maine, USA. This abrupt rather than gradual decrease in tablet thickness could have been due to anaerobiosis-related shell dissolution associated with winter and/or gametogenesis (LUTZ & RHOADS, 1980). However, thinner tablets could also have resulted from faster rates of nacre deposition as water

temperatures increased during this period (WADA, 1961; DIETH, 1985).

The outer shell layer of *Mytilus edulis* is composed of thin calcitic needles between 1 and 3 μm in diameter that are deposited at an angle with respect to the inner surface of the outer layer (TAYLOR *et al.*, 1969). When viewed in polished and etched radial section, the outer shell layer of *M. edulis* is also divided into a series of microgrowth increments (ZOTTOLI & CARRIKER, 1974) that represent alternating periods of shell growth (increments) and growth cessation (increment boundaries) (PANNELLA & MACCLINTOCK, 1968; LUTZ & RHOADS, 1980). Microgrowth increments in bivalve shells reflect exogenous and/or endogenous rhythms that are often highly correlated with cyclic fluctuations in the environment, such as tide, illumination, temperature, *etc.* (see LUTZ & RHOADS, 1980). A microgrowth increment in the outer layer delineates a shell region that was deposited contemporaneously, while a microgrowth increment boundary records the position of the inner surface of the outer layer prior to the deposition of the next microgrowth increment (PANNELLA & MACCLINTOCK, 1968; LUTZ & RHOADS, 1980).

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In this paper, we describe in detail changes in the microstructure of the outer shell layer of *Mytilus edulis* associated with naturally occurring interruptions to growth. The blue mussel is an important species in coastal environmental impact assessment, as evidenced by its use in the "Mussel Watch" program (NATIONAL ACADEMY OF SCIENCES, 1980; FARRINGTON *et al.*, 1983) and numerous studies of the sublethal effects of pollutants (*e.g.*, SUNILA & LINDSTRÖM, 1985; AMIARD *et al.*, 1986; STRÖMGREN *et al.*, 1986). Detailed analyses of blue mussel microstructural shell growth could provide additional information on the timing and sublethal effects of environmental disturbances. Furthermore, information from such neontological studies could be useful in the examination of fossil mytilid shells in paleoecological investigations.

MATERIALS AND METHODS

Mussels were collected approximately every two months from three populations in New Jersey. The first was an intertidal population living on a rock jetty in lower Delaware Bay (38°59'N, 74°58'W). Specimens were collected between 0.5 and 1.0 m above mean low water (MLW). The second population was barely subtidal on the bottom of the Manasquan River (40°06'N, 74°03'W). Water depth at MLW ranged between 0.1 and 0.5 m. The third sampled population, also subtidal, was located in Sandy Hook Bay (40°27'N, 74°03'W) at a MLW depth ranging from 5.2 to 6.4 m. The Delaware Bay population was sampled between April 1986 and May 1987, while the Manasquan River and Sandy Hook populations were sampled between November 1987 and October 1988. Water temperature and salinity at the sampled locations on the days of collection ranged from 6.3 to 27.0°C and from 17.1 to 26.0 ppt (parts per thousand), respectively, in Delaware Bay, 10.4 to 24.0°C and 16.9 to 30.0 ppt, respectively, in Manasquan River, and 7.8 to 20.1°C and 23.7 to 28.2 ppt, respectively, in Sandy Hook Bay.

Shell microstructure was studied by light microscopy of acetate peel replicas of polished and etched shell sections and by scanning electron microscopy (SEM) of fractured shell sections. Soft tissues were carefully removed from each specimen, and shells were numbered, thoroughly washed in tap water, and allowed to dry in air overnight. One valve, embedded in liquid casting plastic to prevent breakage, was sectioned from the umbo to the posterior margin using a Raytech 10-inch circular rock saw. Acetate peels were prepared according to the methods outlined in KENNISH *et al.* (1980). A total of 232 acetate peels of shell sections were analyzed (94 from the Delaware River, 67 from the Manasquan River, and 71 from the Sandy Hook Bay populations). Ranges in shell length and age, respectively, of the specimens analyzed from each site were: (1) Delaware Bay, 11.8–43.4 mm, 0–5 yr; (2) Manasquan River, 18.4–66.3 mm, 0–3 yr; and (3) Sandy Hook Bay, 21.9–71.8 mm, 0–3 yr.

Shell sections for analysis by SEM were prepared by

fracturing the shell by hand as close as possible to the anterior-posterior axis (KENNISH *et al.*, 1980). Shell fragments were glued to aluminum stubs with cyanoacrylate cement and carbon paint, and coated with Au-Pd in a sputter coater. A total of 40 specimens (21 from the Delaware River, 9 from the Manasquan River, and 10 from the Sandy Hook populations) were analyzed at 15 and 20 kV accelerating voltages in a Hitachi S-450 scanning electron microscope. Ranges in shell length and age, respectively, of the specimens analyzed by SEM from each site were: (1) Delaware Bay, 17.7–40.3 mm, 0–5 yr; (2) Manasquan River, 18.4–49.5 mm, 0–3 yr; and (3) Sandy Hook Bay, 21.9–70.9 mm, 0–3 yr.

The angle of prism deposition was defined with respect to the inner surface of the outer shell layer. By definition, prisms deposited at an angle of 0° would have their long axes parallel to the inner surface and terminate at the posterior shell margin. Angles of prism deposition increased in a clockwise direction and were measured directly off scanning electron micrographs of fractured sections with a protractor.

RESULTS AND DISCUSSION

The most obvious seasonal microstructural feature in the outer shell layer of *Mytilus edulis* was the thick growth-cessation mark (microgrowth increment boundary) resulting from a period of dormancy in winter (Figure 1). HILBISH (1986) found that *M. edulis* at similar latitudes in eastern Long Island Sound resumed shell growth in February after a dormant period in December and January. Winter growth-cessation marks divided the outer layer into annual increments. Annual outer layer microstructural sequences were similar for mussels collected from all three populations. With increasing age at each site, however, the size of the annual increment declined. There was also a greater tendency for the portion deposited in fall to be absent as age increased beyond 2–3 yr. Consequently, shell growth became increasingly limited to spring as individuals aged. The time of formation of portions of the outer layer was determined by their proximity to known time-periods in the shell, which included winter marks and the posterior shell margin (date of collection).

There were two seasons, summer and late winter, in which terracing of the shell exterior surface was observed. During both seasons, microgrowth increments tended to extend posteriorly only slightly beyond the one most recently deposited, yielding a blunt, thick posterior margin. Thus, outer layer shell growth in these periods tended to be directed more toward the shell interior than posteriorly, especially when compared with the outer layer deposited in spring and fall. Specimens collected during spring and fall tended to have a thinner, more pointed posterior shell margin, which is also revealed in the pattern of microgrowth increment boundaries in Figure 1. Terracing of the shell exterior surface tended to be more pronounced in mussels collected from Delaware Bay and Manasquan

In the article by Fritz, Ragone, and Lutz in *The Veliger*, Vol. 34, No. 2, pp. 222–228, part of Figure 1 on p. 224 did not get printed due to an error by the printer. The complete figure is printed below.

Trim the figure from this erratum, peel off the back of the paper, and position the figure on p. 224 of the April issue.

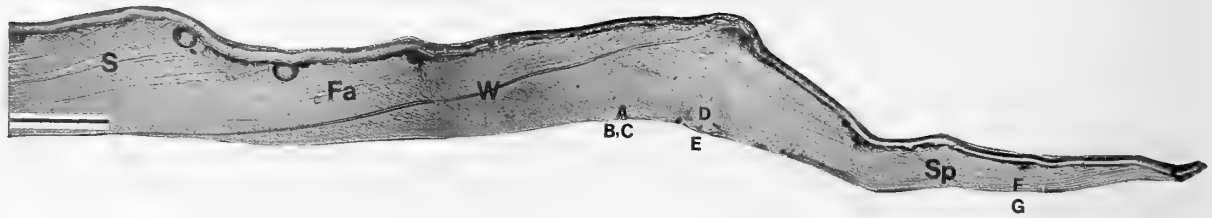


Figure 1

Light micrograph of the acetate peel replica of the outer prismatic shell layer of a specimen of *Mytilus edulis* collected 13 May 1988 from the Manasquan River. The posterior shell margin is at the right; the inner shell surface is at the bottom. S, Fa, W, and Sp denote regions of the outer layer deposited in summer, fall, winter, and spring, respectively. A–G refer to locations where micrographs in Figure 3A–G, respectively, were taken. Scale bar = 500 μm .

River than in those collected from Sandy Hook Bay, perhaps reflecting the greater range in temperature and salinity observed at the two former sites. Furthermore, populations at the Delaware Bay (intertidal) and Manasquan River (barely subtidal, but exposed under certain wind conditions) sites had greater aerial exposure than those in Sandy Hook Bay (continuously submerged). Aerial exposure would increase the range in temperatures to which the animals were actually exposed.

Seasonal changes in the shape of the posterior shell margin were reflected in, and most probably resulted from, seasonal changes in the microstructure of the outer layer. Prismatic needles near the posterior margin in mussels collected in spring and fall were long, evenly shaped, and deposited at angles of about 30° (Figure 2A, B; Table 1). In summer-collected mussels, however, prismatic needles near the posterior margin were stubby or lenticular in shape and deposited at angles ranging from 43 to 80° (Figure 2C, D; Table 1). Little or no shell growth occurred in winter (HILBISH, 1986), which resulted in a growth-cessation mark (Figure 1). The outer layer microstructure (near the posterior margin) of specimens collected in winter resembled that of fall-collected specimens in radial fracture section, but showed signs of dissolution (smoothed, etched, or indistinguishable prism tips) on the inner depositional surface similar to that shown in Figure 2D. Specimens collected in late winter (February), however, had prismatic needles resembling those in Figure 3F and G near the posterior shell margin, indicating that shell growth had resumed.

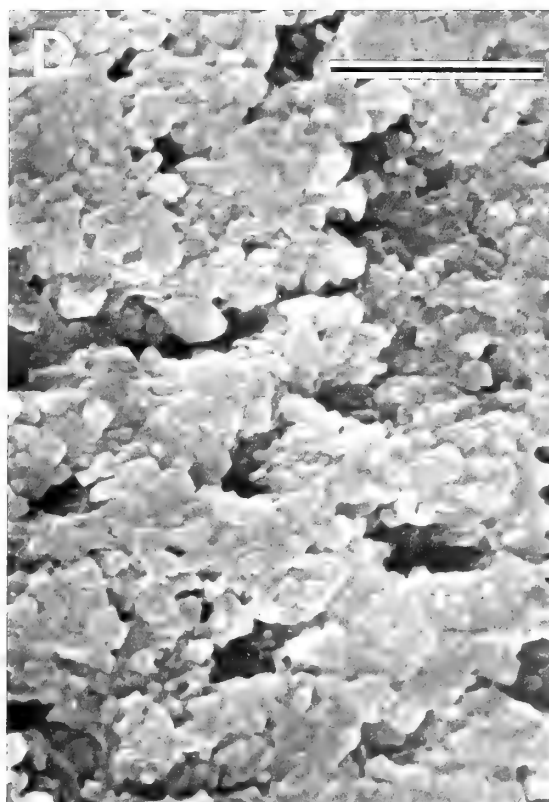
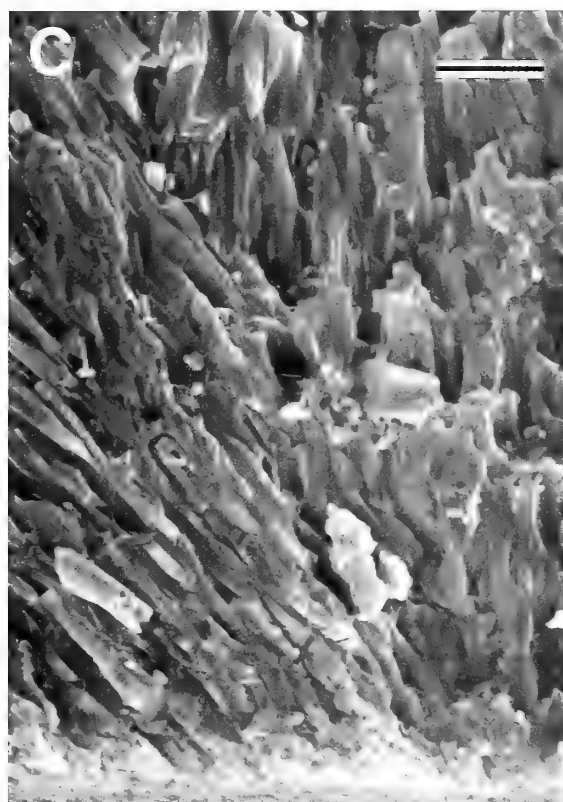
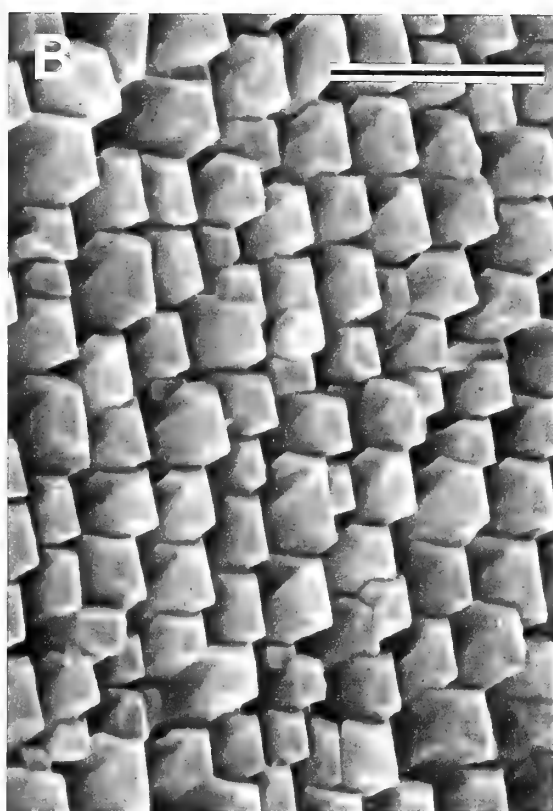
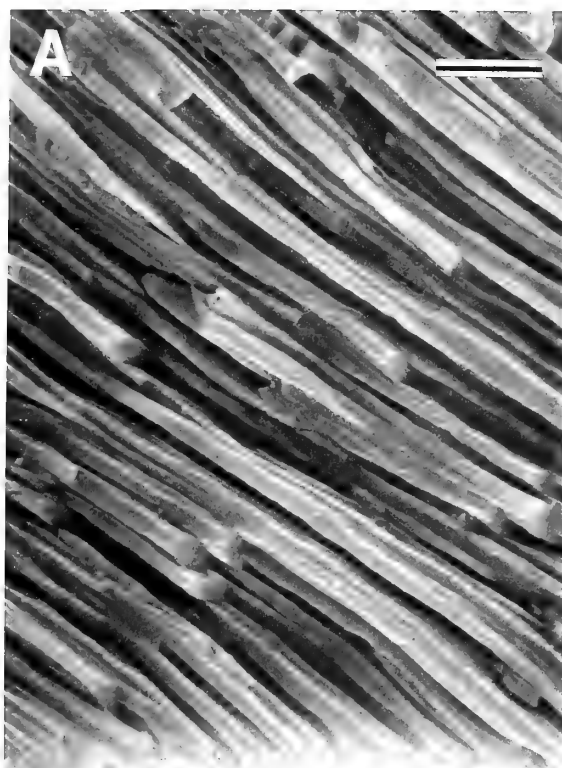
Upon resumption of shell growth in late winter, a cone-shaped region of prisms was formed at the posterior shell margin in which prisms were oriented at angles ranging from 51 to 140° in individual shells (Table 1). Details of

one cone-shaped region formed in late winter by the specimen in Figure 1 are shown in the series of scanning electron micrographs in Figure 3 (note locations where micrographs in Figure 3 were taken on Figure 1) and schematically represented in Figure 4. The prism cone has its apex at the intersection of the winter growth-cessation mark and the shell's exterior surface (T in Figure 4). Prisms in the anterior portion of the cone (Figure 3A–C) were pointed anteriorly and deposited at angles as great as 140° . Prisms in the cone's anterior portion were similar in shape, size, and tip morphology, but not in orientation, to those deposited in spring and fall (Figure 2A, B). Prisms in the center portion of the cone were deposited at angles of about 90° and formed a granular-textured inner surface (Figure 3D, E) similar to that found near the posterior margin in summer (Figure 2C, D). With increasing distance in a posterior direction from the cone's center, prism deposition angle gradually decreased to about 30° near the posterior margin (Figure 3F, G).

The micrographs in Figure 3 were all photographed on or near the inner surface of the outer shell layer; in other words, in different portions of a single microgrowth increment. Thus, prisms in each of the three regions were presumably formed at the same time by different portions of the mantle just prior to collection in May 1988. Posterior portions of the mantle were depositing prisms at angles of about 30° (Figures 3F, 4) at the same time as more anterior portions of the mantle were depositing prisms at about 90° (Figures 3D, 4), 140° (Figures 3A, 4) and 23° (Figures 3A, 4). On the basis of the post-growth-cessation outer layer microstructure of numerous specimens, we hypothesize that prism orientation is initiated at the shell margin. Once prism orientation is initiated, individual prisms continue to be deposited at that angle until the outer layer is

Figure 2

Scanning electron micrographs of radial fracture (A, C) and inner depositional surfaces (B, D) of the outer prismatic shell layer of specimens of *Mytilus edulis* collected from Delaware Bay on 12 November 1986 (A), 19 June 1986 (B), and 14 August 1986 (C, D). Growth is to the right in all micrographs and the inner shell surface is at the bottom of A and C. Scale bars = 4 μm .



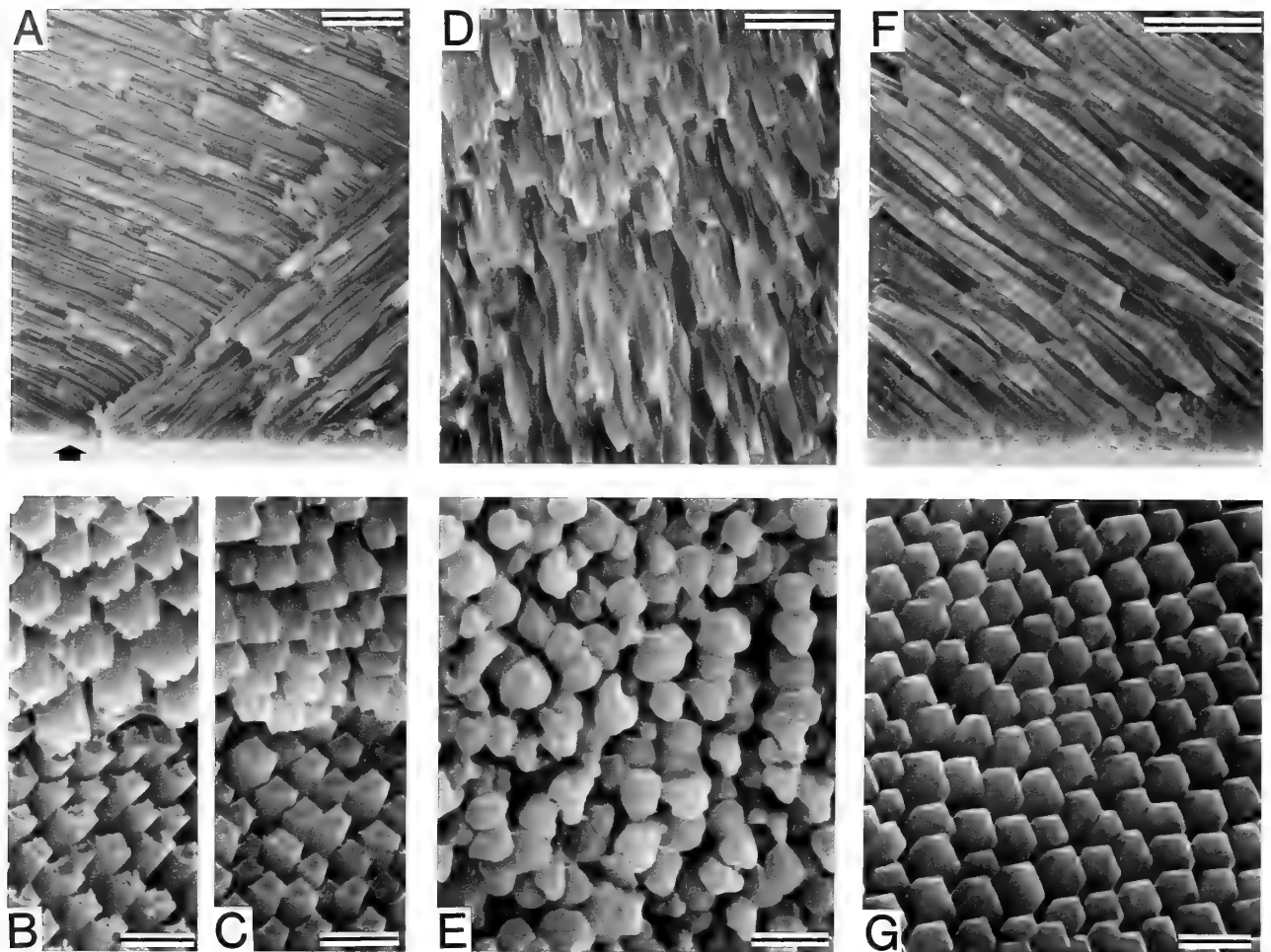


Figure 3

Scanning electron micrographs of radial fracture (A, D, F) and inner depositional surfaces (B, C, E, G) of the outer prismatic shell layer of the specimen of *Mytilus edulis* shown in Figure 1. Micrographs A–G were taken at the locations shown on Figure 1. Arrow in A shows the location along the inner shell surface where B and C were taken. Growth in micrographs A and D–G is to the right; in B and C, growth is up. The inner shell surface is at the bottom of A and F, and parallel with and beyond the bottom of D. Scale bars: A = 10 μm ; B, C, E, G = 2 μm ; D, F = 5 μm .

Table 1

Angle (in degrees; mean and range) of outer layer prism deposition by specimens of *Mytilus edulis* collected in each season from three New Jersey locations. n = number of mussel specimens analyzed.

	Spring	Summer	Fall	Late winter
Mean	31.7	56.0	29.2	83.9
Range	26–45	43–80	20–36	51–140
n	15	9	9	10
Months	Mar.–Jun.	Jul.–Aug.	Sep.–Nov.	Feb.

overlain by the pallial myostracum and the inner shell layer. This scenario explains the different orientation of prisms at various points along the inner surface of the outer layer which were all formed at the same time (present within the same microgrowth increment).

Seasonal changes in the angle of outer layer prism deposition may be responsible for undulations and terracing of the shell's exterior surface in summer and winter (Figure 1). Prism growth can be described by considering the ratio of the posterior (P) and inward (I) vectors of prism growth, P/I, which is equivalent to the inverse of the tangent of the angle of prism deposition. Prisms deposited at angles of 30° have a P/I ratio of 1.73, indicating that outer layer shell growth in the posterior direction is 1.73 times that in the inward direction. This results in sharply pointed posterior shell margins like those formed in spring and fall

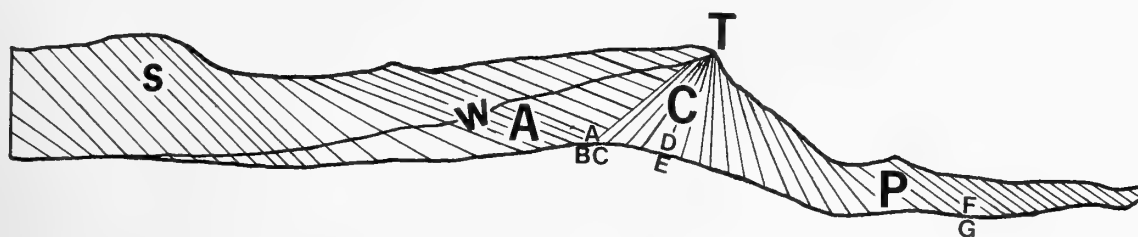


Figure 4

Line drawing showing outer layer prism orientation of the specimen in Figures 1 and 3. Prisms in the cone-shaped region (C) were initiated at the apex of the cone (T) in late winter 1987–1988 after the formation of the winter growth-cessation mark (w). Prisms anterior to the cone (A) were initiated in fall 1987 but deposited in late winter and spring. Prisms in the posterior region (P) were initiated and deposited in spring 1988. Scale and other notation as in Figure 1.

(Figures 1, 4; Table 1). At prism deposition angles of greater than 45° , the P/I ratio is <1 , resulting in a more blunt posterior margin similar to that formed in summer (Figures 1, 4), which had a mean prism deposition angle of 56° (Table 1). As prism angles approach 90° , like those found in the center axis of the cone, then P/I approaches 0, yielding the steeply terraced shell exteriors found posterior to winter growth-cessation marks (Figures 1, 4).

Other researchers (TAYLOR *et al.*, 1969; TRAVIS & GONSALVES, 1969; GRÉGOIRE, 1972; CARRIKER, 1978; CARTER, 1980) have observed that prism orientation with respect to the inner shell surface is not the same across the entire cross-sectional surface of the outer layer of *Mytilus edulis*. TAYLOR *et al.* (1969) described calcitic prisms that were "arranged into larger units, which appear[ed] to be broadly triangular in section but which [had] a conical form in three dimensions. Within these conical units, the needles radiate[d] from the apex of the cone, which point[ed] outwards towards the exterior of the shell. These broader units [were] developed quite sporadically in any one shell" (p. 81). The conically shaped regions described by TAYLOR *et al.* (1969) are similar to those described here that were associated with seasonal changes in shell growth rates and resulted in undulations and terraces in the shell exterior. Regions of steeply angled prisms can also result from other disruptions to growth severe enough to form growth-cessation marks, such as those resulting from thermal effluents (KENNISH & OLSSON, 1975) or storms (FRITZ & LUTZ, 1986) identified in the shell microstructure of other bivalve species. Analyses of the outer layer microstructure of *M. edulis* could provide a record of the timing and possible severity of each disruption, creating a tool for sublethal environmental impact assessment.

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NOTES, INFORMATION & NEWS

Sexual Dimorphism in *Castalia undosa undosa*

Martens, 1827 (Bivalvia: Hyriidae)

by

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The entire gamut of sex differentiation can be found among bivalves, from species with strictly separate sexes to species that are "almost invariably functionally hermaphroditic" (COE, 1943). In general, South American freshwater bivalves are reported to be dioecious species with no distinction between males and females in terms of shell shape characteristics. ORTMAN (1921a) has reported that the sex of certain species of North American *Lampsilis* and *Truncilla* can be determined on the basis of shell shape. According to COE (1943), for certain dioecious species of *Unio* and *Astarte*, the two sexes can be distinguished by shell shape in adult animals. ORTMAN (1921b) did not record any case of hermaphroditism for South American naiades or shell traits that might distinguish males from females.

In the South American bivalve families Hyriidae and Mycetopodidae, hermaphroditism was recorded for *Anodontites trapesalis* Lamarck, 1819, and *Anodontites trapezeus* Spix, 1827, by HEBLING (1976), and for *Mycetopoda legumen* Martens, 1888, by VEITENHEIMER & MANSUR, (1978). According to BONETTO (1951), hermaphroditism is common in the genus *Anodontites*. Among Hyriidae, hermaphroditism was observed in *Diplodon delotundus expansus* Kuster, 1865 (CURIAL & LANGE, 1974) and in *Diplodon rotundus gratus* Wagner, 1827 (HEBLING & PENTEADO, 1974).

Gonochorism with no macroscopic distinction between males and females was observed in *Diplodon chilensis chilensis* (Gray) by PEREDO & PARADA (1984). BONETTO (1965), in a review of the tribe Cristallini, reported no data concerning bivalve sexuality. MANSUR (1972), studying the morphology of the digestive tract of *Castalia undosa martensi* Ihering, 1891, made no mention of sex. OLIVEIRA (1985), when studying the gametogenic cycle of *C. undosa undosa* Martens, 1827, found only two hermaphroditic specimens.

While studying the functional anatomy of *Castalia undosa undosa*, we noticed that the shells of dissected animals

differed in beak conformation (posterior region of the animal), with some of them exhibiting acute angles and others rounded angles. Thus, the objective of the present study was to determine the existence of sexual differences between male and female *C. undosa undosa*, manifested as a posteroventral deflection of the shell in males that renders the region pointed.

This is the first study demonstrating the presence of sexual dimorphism in the adult shell among freshwater bivalves from South America, providing data that will contribute to our knowledge about *Castalia undosa undosa*.

Materials and Methods

Live specimens of *Castalia undosa undosa* were collected from the Pardo River in the municipality of Ribeirão Preto (21°07'S and 47°45'W), state of São Paulo, Brazil. The animals live buried in muddy substrates, usually under the shade of bushes and trees or among the roots of aquatic plants, and can be captured only by probing the river bottom with the feet or the hands. Lots of 25 animals each were collected at random at different sites at three-month intervals for a total of 100 specimens, and carried to the laboratory where they were anesthetized with magnesium chloride and fixed in Bouin's for histological examination.

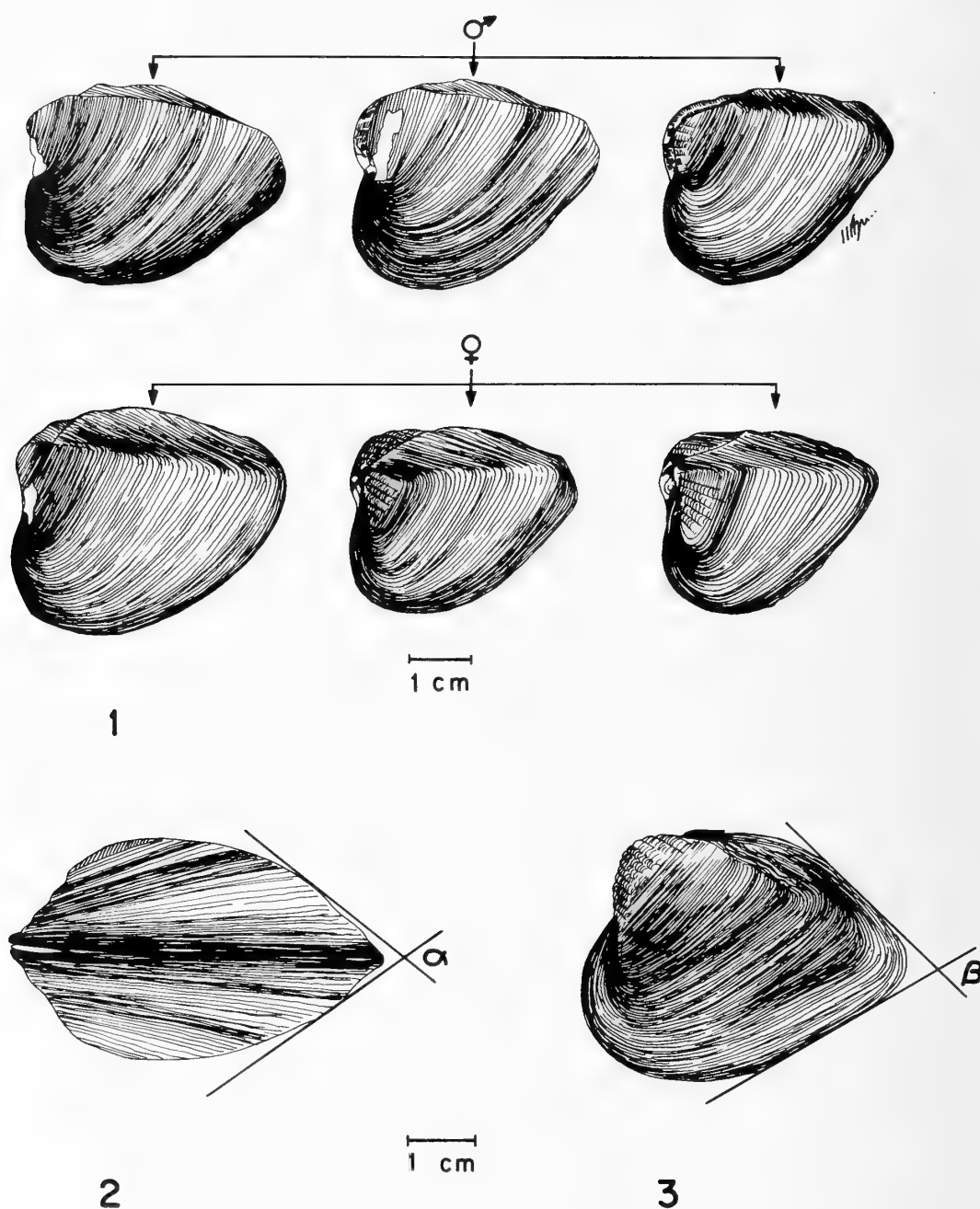
The animals were divided into two groups according to conformation of the shell beak. Group 1 consisted of animals showing a sharp-pointed shell beak, and group 2 consisted of animals with a rounded shell beak (Figure 1). The transverse (Figure 2) and longitudinal (Figure 3) angular apertures of each shell were measured with the aid of a fixed spindle transferer, and a gonad biopsy was taken from each animal.

The 100 specimens were sectioned transversely at the level of the region posterior to the stomach and the posterior half was dehydrated and embedded in paraffin. Approximately twelve 10- μ m-thick histological sections were cut transversely, alternated every 5 mm, and stained with hematoxylin-eosin. The purpose of this procedure was to certify the sex and to determine the arrangement of male and female follicles in the visceral mass. The sex of each animal was determined by light microscopy. Data were analyzed statistically by the Student *t*-test.

Results and Discussion

Of the specimens of *Castalia undosa undosa* collected, 52 were females and 48 males. Mean female length was 6.03 cm and mean male length was 6.35, with a mean overall size for males and females of 6.19 cm. The smallest specimen was 4.43 cm long and the largest 7.6 cm.

The mean (\pm SEM) transverse angular aperture was 64.8 ± 0.65 for females and 6.4 ± 0.66 for males, and the



Explanation of Figures 1 to 3

Figures 1-3. *Castalia undosa undosa*. Figure 1. Drawing of the left valves of males and females showing the differences between them. Figure 2. Ventral view of the shell to show the transverse angle (α). Figure 3. Lateral view of left valve to show the longitudinal angle (β).

mean longitudinal angular aperture was 67.7 ± 0.65 for females and 64.3 ± 0.56 for males. It can be seen that both values were larger for females than for males, with statistically significant differences in both cases ($P < 0.001$).

When sex determination was attempted visually with the unaided eye without using a fixed spindle transferrer,

the error for the 100 specimens was on the order of 16%. The error occurred especially for young specimens measuring less than 5 cm, because in these juveniles the posteroventral deflexion of the shell is not as evident. In South American freshwater dioecious bivalves, dimorphism is usually observed macroscopically when the marsupium of

pregnant females is full of eggs or embryos during the spawning phase. At any other time (*i.e.*, during the phases preceding or following spawning) a gonad biopsy is needed to identify the sexes.

According to COE (1943), in some species the functional sex phase of some or all individuals may change throughout the life of the animals. In this respect, we used as a starting point a study by OLIVEIRA (1985) who determined the annual gametogenesis cycle of *Castalia undosa undosa* in an investigation of 120 adult animals in which she only detected two hermaphrodite specimens. In a study of the functional anatomy of *C. undosa undosa*, AVELAR & SANTOS (1991) found no cases of hermaphroditism. No such cases were detected among the 100 specimens studied in the present investigation. The ideal approach would be to study juveniles of *C. undosa undosa* in which the dimorphic shell trait is still not manifested in order to observe the definition of sexuality.

On the basis of the present results, we conclude that the sexuality of *Costalia undosa undosa* can be determined by the shape of the shell in adult animals in which the posterior beak of the valves presents smaller transverse and longitudinal angles in males than in females.

Our research was supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), grant No. 500083/88-6. We are grateful to M. S. Ribeiro for the drawings.

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International Commission on Zoological Nomenclature

The following applications were published on 29 June 1990 in Vol. 47, Part 2 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

Case 2630—*Helix* (*Helicigona*) *barbata* Férussac, 1832 (currently *Lindholmiola barbata*; Mollusca, Gastropoda): proposed confirmation of lectotype designation. Brought by D. Kadolsky.

Case 2699—Rissooidea (or Rissoacea) Gray, 1847 (Mollusca, Gastropoda): proposed precedence over Truncatelloidea (or Truncatellacea) Gray, 1840. Brought by G. Rosenberg and G. M. Davis.

Case 1643—*Mytilus anatinus* Linnaeus, 1758 (currently *Anodonta anatina*; Mollusca, Bivalvia): proposed designation of a neotype. Brought by P. B. Mordan and F. R. Woodward.

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First Congress of Latin American Malacology

The First Congress of Latin American Malacology is scheduled to be held in Caracas, Venezuela, from 15 to 19 July 1992. Field trips to four different areas are scheduled on the 19th and 20th. Official languages include Spanish, Portuguese, and English. Sessions will be held on general malacology and applied malacology, the latter with a special focus on *Strombus gigas*.

For more information, write to: Lic. Roberto Cipriani, Universidad Simón Bolívar, Apartado Postal 89.000, Caracas 1080, Venezuela.

BOOKS, PERIODICALS & PAMPHLETS

A Systematic and Bibliographic List of the Japanese Land Snails

by HIROSHI MINATO. 1988 (August 8). Nihon Rikusan Kairui Soumokuroku Kankokai, Shirahama, Japan. ix + 294 pp.

The fundamentals of the Japanese land mollusk fauna are now readily accessible, between this book for the literature and *Colored Illustrations of the Land Snails of Japan*, by Masao Azuma (Ōsaka, Hoikusha Publishing Company, 1982), for pictures and identification. Few other land snail faunas (and none of comparable geographic extent) are so concisely covered. Only an atlas of range maps would be needed to give a complete, basic picture.

This work provides synonymies for all the land mollusks known from Japan, including the Ryukyu Islands. References to each species are in chronological order. Authors' names and journal titles (even those of Asian origin) are in Roman characters, which, theoretically, should make it

possible to access all of the pertinent literature. (In the terminal bibliography, works by Asian authors, including authors' names, appear only in *kanji* characters; hence an American-speaker like me cannot just flip to the back and get the complete reference to a paper of interest.)

The classification generally follows that of Solem (pp. 49–97 in V. Fretter & J. Peake, eds., *Pulmonates*, Vol. 2A. *Systematics, Evolution and Ecology*. London, Academic Press, 1978). One new taxon is proposed, the subfamily Euhadrinae of Bradybaenidae, based on *Euhadra* Pilsbry, 1890. There is no statement of characters purporting to differentiate it from other taxa (or reference to such a statement) and Euhadrinae therefore is probably a *nomen nudum*. It would have been interesting to know in what respect this subfamily was thought to differ from, for example, Bradybaeninae, Aegistinae, or the recently proposed Monadeniinae Nordsieck, 1987.

Barry Roth

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Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, not justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

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Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

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Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

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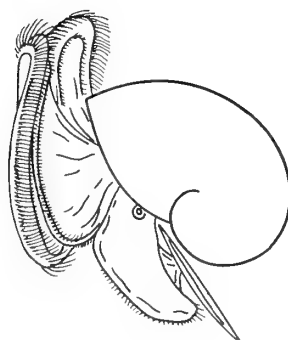
Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

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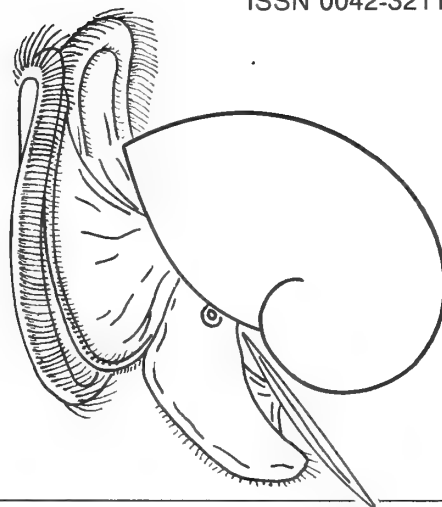
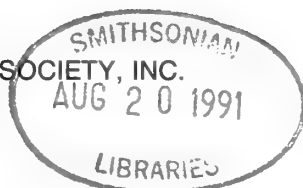
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The Veliger (ISSN 0042-3211) is published quarterly on the first day of January, April, July, and October. Rates for Volume 34 are \$28.00 for affiliate members (including domestic mailing charges) and \$58.00 for libraries and nonmembers (including domestic mailing charges). For subscriptions sent to Canada and Mexico, add US \$4.00; for subscriptions sent to addresses outside of North America, add US \$8.00, which includes air-expedited delivery. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Museum of Paleontology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to The Veliger, Museum of Paleontology, University of California, Berkeley, CA 94720.

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The Veliger is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, evolutionary, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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Distribution and Diversity Patterns of Australian Pupilloid Land Snails (Mollusca: Pulmonata: Pupillidae, s.l.)

by

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Department of Zoology, Field Museum of Natural History, Roosevelt Road and Lake Shore Drive,
Chicago, Illinois 60605-2496, USA

Abstract. Data are presented on the distribution and diversity patterns of 34 native Australian pupilloid land snails. In addition, mention is made of two introduced species. Most Queensland and New South Wales species have not been revised and distributional data for these taxa are sparse. Therefore, they are not included. Eight of the nine genera range outside of Australia. The monotypic *Glyptopupoides* Pilsbry, 1926, is the only restricted endemic. Four of the 34 native species also live in Indonesia or New Guinea.

The south and west coasts of Australia have a limited fauna of three genera and four restricted endemic species each, plus a minor intrusion of *Gastrocopta deserti* Pilsbry, 1917, from the "Red Centre." No pupilloids have been collected in the humid southwestern corner of Western Australia, Tasmania, or most of Victoria. The "Red Centre" has seven species, two with quite restricted ranges, in three genera. One "Red Centre" species, *G. deserti*, has the widest range of any Australian pupilloid, extending from western Queensland to the North West Cape in Western Australia, as far north as the south fringes of the Kimberley, and then south to the Flinders Ranges in South Australia.

The Kimberley in Western Australia and the "Top End" of the Northern Territory have the greatest diversity in both genera and species, with eight genera and 19 species present. Local distribution in this region is rather complex and correlates mainly with moisture regimes.

Patterns of local diversity also are discussed.

INTRODUCTION

† **Editor's note:** Several weeks before his death on 26 February 1990, Alan Solem mentioned to one of his colleagues at the Field Museum, Vickie Huff, that he was working on "the pupillid range paper" at home and that he had one part to finish before submitting it to *The Veliger*. Regrettably, he did not have the opportunity. Ms. Huff, however, was able to gather all of the previously completed, computer-generated figures and to retrieve the text from Alan's computer. She submitted the posthumous manuscript to *The Veliger* in accordance with Alan's expressed intent; it was evaluated by three reviewers, and accepted for publication. Although we suppose that the manuscript was nearly complete, readers may notice a few places where Alan was likely to have returned to fill in a section or to make a revision. Nevertheless, only minor editorial changes were made in the submitted manuscript in order to preserve, as much as possible, the author's intent. After the initial manuscript submission, Margaret Baker of the Field Museum took over the responsibility of seeing the project through to completion. Without her considerable efforts we would not now have the opportunity to read Alan Solem's last contribution to science. D.W.P.

As a by-product from extensive field surveys of the camaenid land snails found in the western two-thirds of Australia, collections of the small-sized and much less diverse non-camaenid families have been accumulated. Pupilloid taxa proved to be especially abundant and moderately diverse. Their shells provide a wealth of characters for species delineation. It was thus possible to review the species found in Australia and determine if they have extralimital ranges. In the absence of any contemporary generic or family level phylogenetic hypotheses and anatomical data on the Australian taxa, it proved impossible to expand these studies into reviews of generic affinities or historical biogeography.

The systematic bases for this study are the survey of Australian members of the basically Southeast Asian-Indonesian genus *Glyptotrachela* Tomlin, 1930 (see SOLEM, 1981); a faunal review of pupilloid species from the south

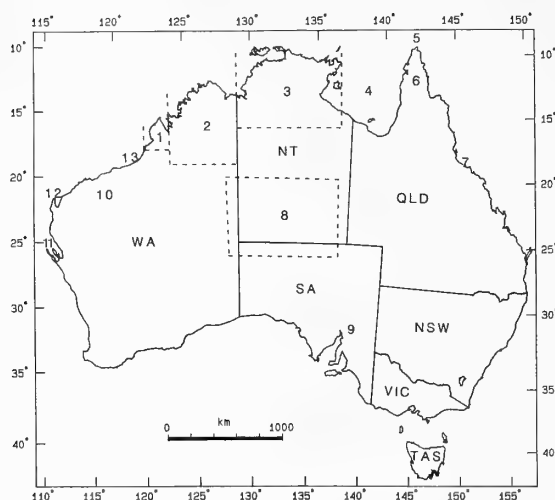


Figure 1

Map of Australia showing approximate outlines of regions discussed in text: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia; 1, Dampierland; 2, Kimberley; 3, "Top End"; 4, Gulf of Carpentaria; 5, Torres Strait; 6, Cape York Peninsula; 7, Townsville, QLD; 8, "Red Centre"; 9, Flinders Ranges; 10, Pilbara; 11, Shark Bay; 12, North West Cape; 13, 80 Mile Beach.

and west coasts of Australia (see SOLEM, 1986); and a monographic review of all non-camaenid land snails from the Kimberley region of Western Australia and all of the Northern Territory (see SOLEM, 1989).

These studies not only greatly extended the known ranges of most taxa and resulted in recognition of several new ones, but permitted preparing the first comprehensive set of distributional maps for any Australian land snail family (Figures 2–32). The patterns of both distribution and diversity were unexpected. The extent to which there are

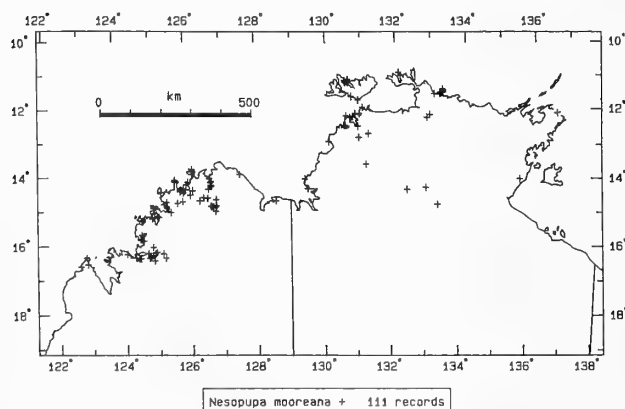


Figure 2

Records of *Nesopupa mooreana* in the Kimberley and "Top End."

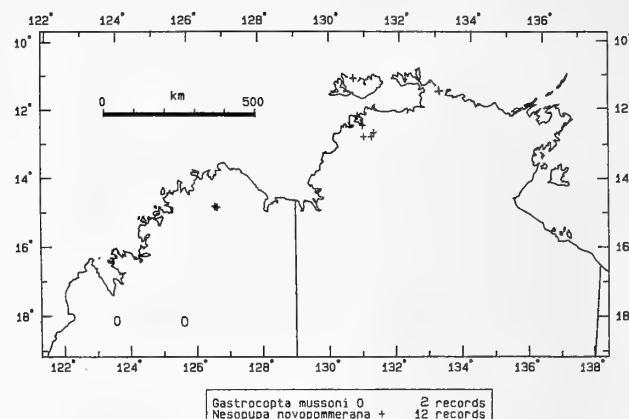


Figure 3

Records of *Nesopupa novopommerana* and *Gastrocopta mussoni* in the Kimberley and "Top End." *Nesopupa novopommerana* has been recorded from New Britain, Bismarck Archipelago, and Tanimbar Island. *Gastrocopta mussoni* has been recorded elsewhere only from Mt. Morgan, Queensland.

extralimital records for both genera and species was equally surprising.

I recognize 34 native (32 named) and two introduced species that belong to eight genera. Some additional taxa were collected in the Cape York Peninsula and along the Gulf of Carpentaria in a 1988 survey. Although brief mention is made of them below, it was not possible to prepare formal descriptions or add their localities to the distribution maps at this time.

A list of the recognized taxa and references to recent literature and illustrations are given in Appendix 1. One additional genus, the Queensland to New South Wales plus New Caledonia *Cylindrovertilla* O. Boettger, 1880,

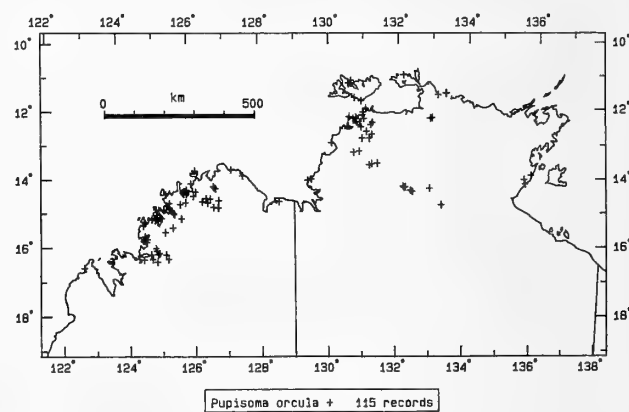


Figure 4

Records of *Pupaia orcula* in the Kimberley and "Top End." Extralimital range is from India and Japan to New Guinea, Hawaii, and Tuamotu Islands.

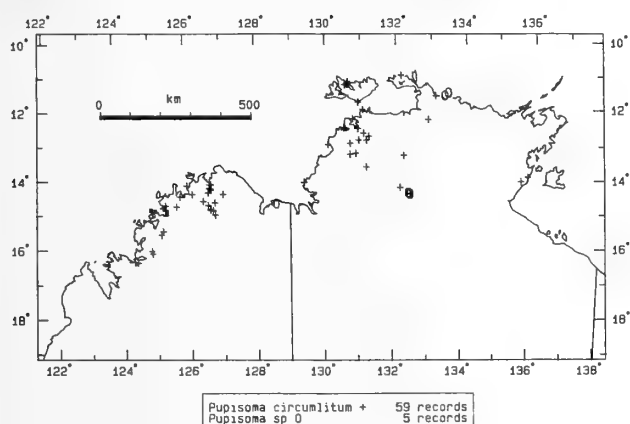


Figure 5

Records of *Pupisoma circumlitum* and *Pupisoma* sp. in the Kimberley and "Top End." *Pupisoma circumlitum* is found also from the Gulf of Carpentaria and Torres Strait south as far as Grafton, New South Wales. *Pupisoma* sp. has not been recorded elsewhere.

could not be reviewed because of limited material in collections; and two unquestionably valid New South Wales species, *Gastrocopta strangeana* Iredale, 1937 (= *strangei* Pfeiffer, 1854, non Benson, 1853) and *Gastrocopta hedleyi* Pilsbry, 1917, are omitted for the same reason. References to these, and a few additional names that probably are synonyms, also are listed in Appendix 1.

PREVIOUS STUDIES

The classic world monograph of the pupilloid land snails included systematic reviews of Australian taxa (PILSBRY,

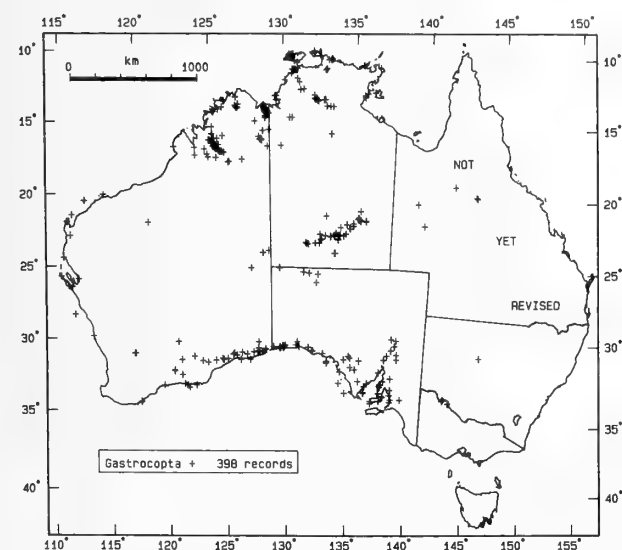


Figure 6

Records of *Gastrocopta* in Australia (revised species only).

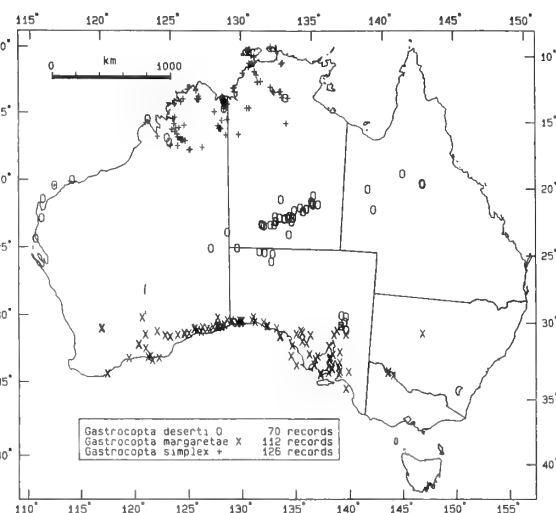


Figure 7

All confirmed records of *Gastrocopta deserti*, *G. margaretae*, and *G. simplex*.

1916–1918; 1920–1921; 1922–1926). Pilsbry provided excellent illustrations, a masterly review of previous literature, and many comments about affinities of the Australian species. Very little anatomical data was available for any pupilloids, and none for members of the Australian fauna.

A biogeographic summary of the pupilloid taxa was presented in PILSBRY (1934–1935:139–169). His opening statement is worth repeating: "The family Pupillidae is

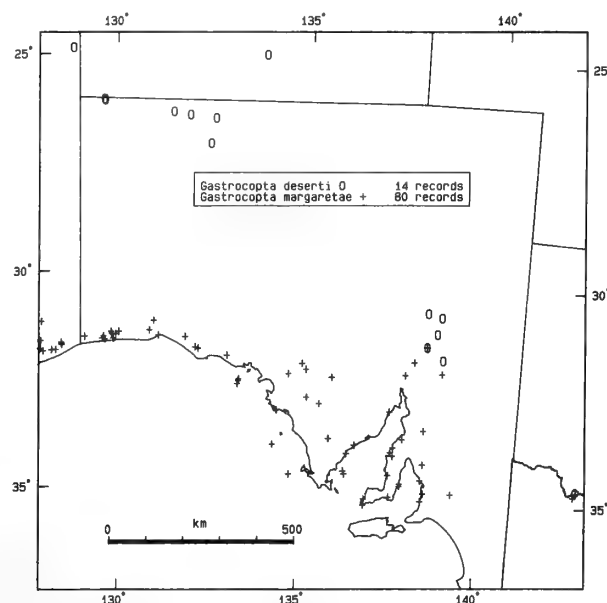


Figure 8

Records of *Gastrocopta deserti* and *G. margaretae* in South Australia and bordering areas.

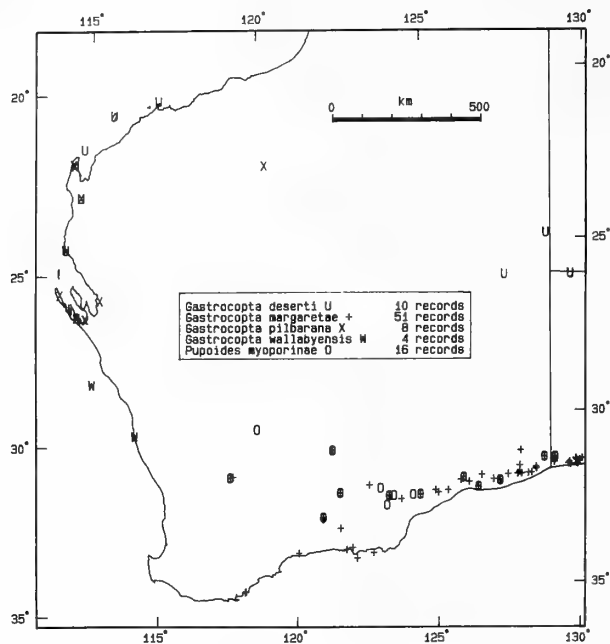


Figure 9

Records of *Gastrocopta deserti*, *G. margaretae*, *G. pilbarana*, *G. wallabyensis*, and *Pupoides myoporinae* in Western Australia below 80 Mile Beach.

essentially a group of the northern continents. The data now at hand indicate Eurasia as the main area of evolution and radiation. All of the major groups (subfamilies) occur in this continent. Of about 50 genera recognized in the family, 38, or about 75 percent, are represented in Eurasia, either living or as Tertiary fossils."

"The southern continents and islands have, in addition to northern genera which extend into them, only about 8

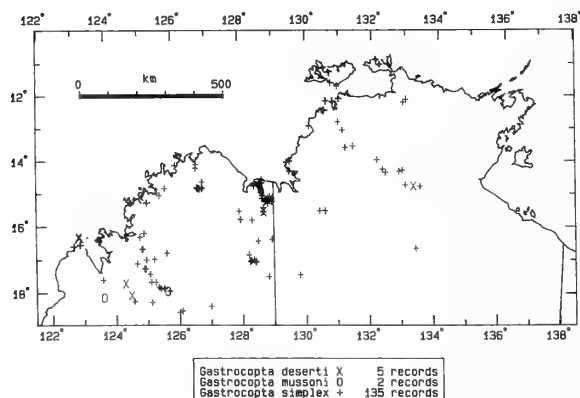


Figure 10

Records of *Gastrocopta deserti*, *G. mussoni*, and *G. simplex* in the Kimberley and "Top End."

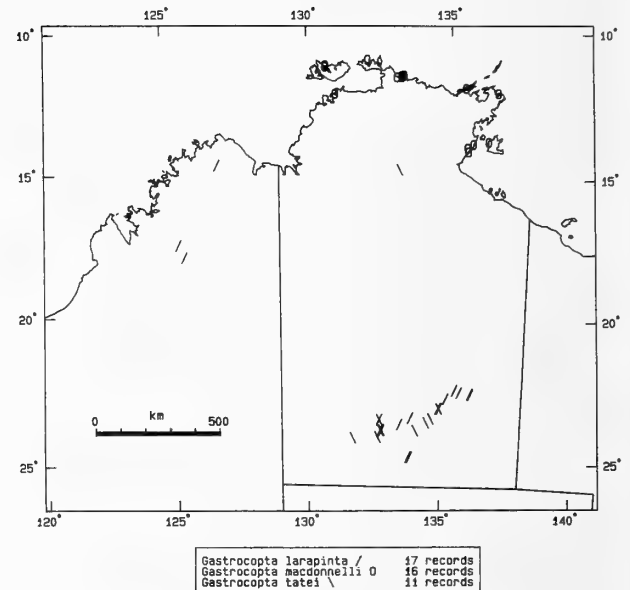


Figure 11

Records of *Gastrocopta larapinta*, *G. macdonnelli*, and *G. tatei* in the Kimberley and Northern Territory. *Gastrocopta macdonnelli* also occurs from Torres Strait to Townsville, Queensland.

endemic genera. . . . There is no trace of Antarctic elements suggesting dispersal via Antarctica" (PILSBRY, 1934-1935: 139-140).

In a series of nomenclatural notes, checklists, and faunal surveys, IREDALE (1930, 1933, 1937a, b, 1939, 1940, 1941)

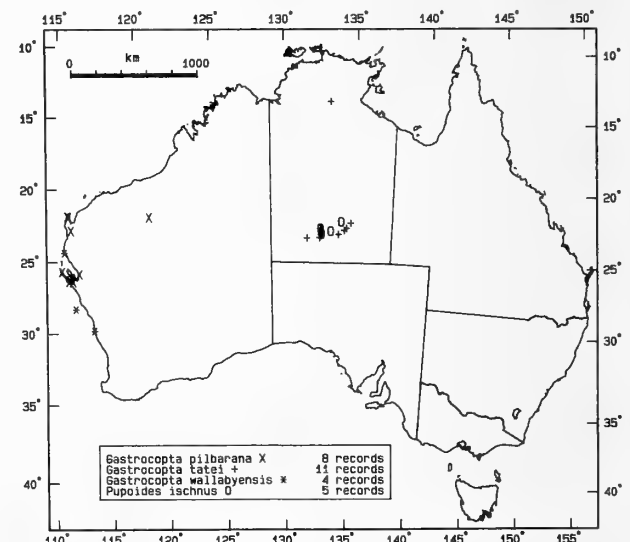


Figure 12

Records of rare Australian species: *Gastrocopta pilbarana*, *G. tatei*, *G. wallabyensis*, and *Pupoides ischnus*.

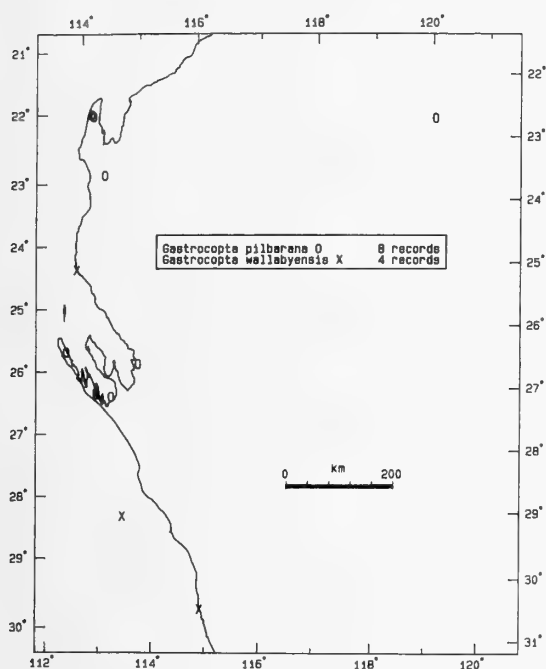


Figure 13

Records of *Gastrocopta pilbarana* and *G. wallabyensis* along the coast of central Western Australia.

proposed eight new generic units (*Famarinia*, *Gyrodaria*, *Imputegula*, *Omegapilla*, *Papualbinula*, *Somniopupa*, *Themapupa*, and *Wallivertilla*); 12 new species or subspecies; and one replacement name (*Gastrocopta strangeana*). The net effect of the generic names was to "isolate" the Australian taxa from those living elsewhere. None of Iredale's new genera are considered valid, and 11 of his 12 new taxa are placed in synonymy. The 12th, *Cylindrovertilla fabreana boynensis* Iredale, 1937, may prove to be valid. His replacement name is accepted.

In the period since Iredale's taxonomic splitting, the Australian pupilloids have had brief biogeographic mention in McMICHAEL & IREDALE (1969) and BISHOP (1981: 934-936, 940); cursory comments in the faunistic handbooks of SMITH & KERSHAW (1979:102-110; 1981:65, 1926); a brief historical review of knowledge concerning the South Australian land mollusks (SMITH, 1985); and the three revisions by SOLEM (1981, 1986, 1989).

No anatomical data have been recorded, leaving questions of both family and generic level classification and phylogeny completely unanswerable at this time. The degree of classificatory uncertainty is demonstrated by Table 1, which lists the family level units of pupilloids used for Australian taxa in the last half century. Table 2 allocates the Australian genera to the subfamilies used in the conservative classification of PILSBRY (1948), which I have chosen to follow in this study. It is not possible to suggest ancestor-descendant relationships among these genera or

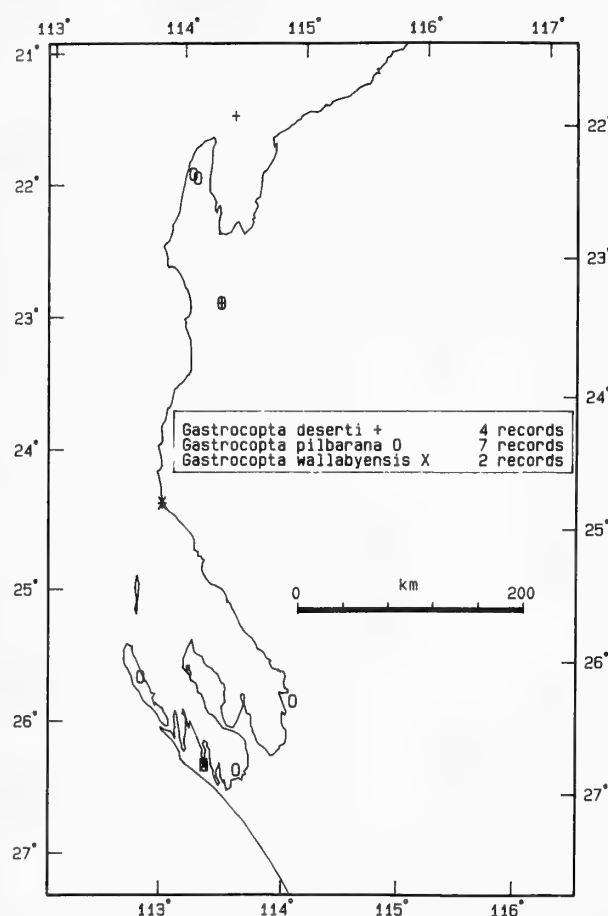


Figure 14

Records of *Gastrocopta deserti*, *G. pilbarana*, and *G. wallabyensis* in Western Australia between Shark Bay and the North West Cape.

to construct meaningful phylogenies. The few published anatomical studies on Holarctic taxa do show that considerable structural variation exists, but too few taxa have been studied to permit phylogenetic studies of the main Holarctic groups, much less the world fauna.

MATERIALS

All records utilized in this study are based upon specimens examined by the author. The early literature contains many misidentifications, and thus only specimen-confirmed localities have been included. The records listed by SOLEM (1981, 1986, 1989) have been supplemented by a review of the collections in the Western Australian Museum, Perth; South Australian Museum, Adelaide; Australian Museum, Sydney; Museum of Victoria, Melbourne; Queensland Museum, Brisbane; and the private collections of Fred Aslin (Mount Gambier, South Australia) and Vince Kessner (Adelaide River, Northern Territory). Extensive collections in 1988 from continental shelf islands along the

Table 1
Previous family level classifications of pupilloid taxa.

IREDALE (1940)	PILSBRY (1948)	ZILCH (1959)	SOLEM (1978)	TILLIER (1989)
Gastrocoptidae	Pupillidae	Pupillacea	Pupillacea	Pupillacea
Cylindrovertillidae	Nesopupinae	Vertiginidae	Pupillidae	Pupillidae
Pupoididae	Gastrocoptinae	Nesopupinae		Chondrinoidea
Pupisomidae	Pupillinae	Gastrocoptinae		Chondrinidae
		Hypselostominae		Vertiginidae
		Pupillidae		
		Pupillinae		
		Valloniidae		
		Acanthinulinae		

Kimberley coast by Vince Kessner and Alan Longbottom; in the Napier and Oscar Ranges in the south Kimberley by R. A. D. Cameron; and the Gulf of Carpentaria and Cape York Peninsula by L. Price, V. Kessner, and J. Stanisc are referred to in the text, but were received for study too late to be added to the maps.

METHODS

All distributional records with good locality data were entered into the FLORAPLOT program at the Western Australian Wildlife Research Centre, Wanneroo, Western Australia. (A hard copy printout of all entered records is located in the Division of Invertebrates, Field Museum of Natural History, Chicago, Illinois.) They were entered to the nearest minute of longitude and latitude if a town, mountain, or homestead was involved or to the nearest second of longitude and latitude if the locality data were more precise, *i.e.*, a spring, creek bend, isolated hill, dam, or well. Localities such as Roebuck Bay, the type locality of *Nesopupa mooreana* (E. A. Smith, 1894), and "Murray River," could not be localized within a minute of latitude and longitude, and thus are not included in the data base.

Table 2

Classification used for Australian pupilloid genera.

Family Pupillidae
Subfamily Nesopupinae
<i>Nesopupa</i>
<i>Pupisoma</i>
<i>Cylindrovertilla</i>
Subfamily Gastrocoptinae
<i>Gastrocopta</i>
<i>Pumilicopta</i>
<i>Gyliotrachela</i>
Subfamily Pupillinae
<i>Pupilla</i>
<i>Pupoides</i>
<i>Glyptopupoides</i>

Maps were printed using a Hewlett-Packard digital plotter. (All printed maps are now located in the Division of Invertebrates, Field Museum of Natural History.) Many maps were designed to indicate broad scale distributions (Figures 2-7, for example), others to show details of diversity and species sympatry (Figures 9, 11, 13, 14, 27, 28, 31). Judicious selection of compatible symbols for different species, such as "+" and "0" or "/" and "\", means that microsympatry to within a second of latitude and longitude appears on the maps as an "⊕" or an "×". Species with complex diversity associations or very wide distributions may thus appear on several maps. Other species may be used as convenient "markers" on several maps against which to compare distributions of widely dispersed species whose many overlapping records would make joint display on one map extremely confusing or incomprehensible.

DISTRIBUTION PATTERNS

Some area terms will not be familiar to non-Australian readers. The following definitions should suffice (see Figure 1):

Dampierland—Peninsula in Western Australian from Broome to Cape Leveque, ca. 16° to 18°S, 122° to 123°30'E.

Kimberley—The northern portion of Western Australia, 13°30' to 19°S, 123°30' to 120°E.

"Red Centre"—Mountainous parts of Western Australia, South Australia, and Northern Territory, 20° to 26°S, 128° to 137°E.

"Top End"—Tropical area of the Northern Territory above the Roper River, ca. 10° to 16°S, 129° to 137°E.

It is easy to forget that Australia is essentially identical in size to the mainland United States (exclusive of Alaska). Despite the number of records, faunal surveys are still very incomplete. Thus, initial commentary must be made as to the adequacy of distributional data and whether blank spots on a map indicate species absence, collecting absence, or revisionary work absence.

Plotted distributions of two genera, *Gastrocopta* Wol-

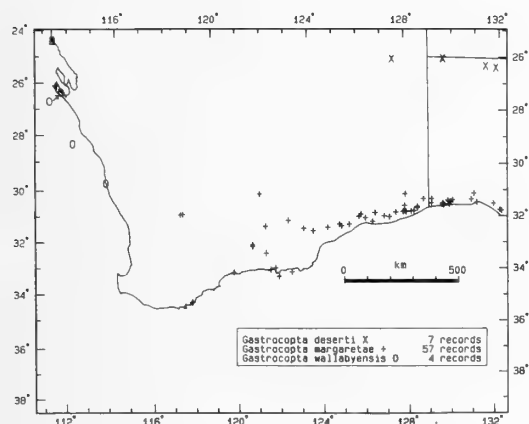


Figure 15

Records of *Gastrocopta deserti*, *G. margaretae*, and *G. wallabyensis* in southern Western Australia.

laston, 1878 (Figure 6) and *Pupoides* Pfeiffer, 1854 (Figure 24), illustrate the above points. *Pupoides* has been recorded from many localities in coastal Queensland and eastern New South Wales, whereas *Gastrocopta* appears to be absent from these areas. In fact, the material of *Gastrocopta* from these regions is somewhat limited [except for the introduced *G. pediculus* (Shuttleworth, 1852)], but the species have not been revised. Neither genus is present in Tasmania or nearly all of Victoria, nor in the humid southwest corner of Western Australia (except for a few islands). Collecting in these regions has been extensive, so that "genus absence" can be accepted. Neither genus shows extensive records along the west side of the Cape York Peninsula and Gulf of Carpentaria. Collections from these areas made late in 1988 contain both genera, indicating that this was a collecting gap.

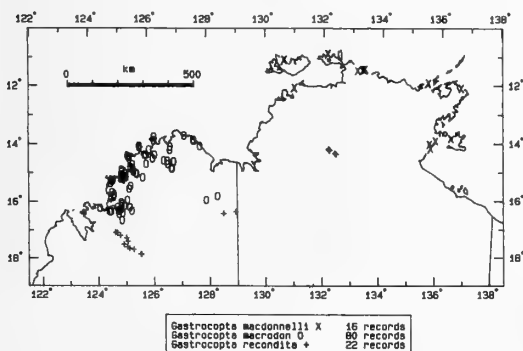


Figure 16

Records of *Gastrocopta macdonnelli*, *G. macrodon*, and *G. recondita* in the Kimberley and "Top End." *Gastrocopta macdonnelli* also ranges from Torres Strait to Townsville, Queensland; *G. macrodon* has been found at Milne Bay, Papua, and in the Louisiade Archipelago; and *G. recondita* is recorded from the Aru and Tanimbar Islands, plus Haruku near Ambon, Indonesia.

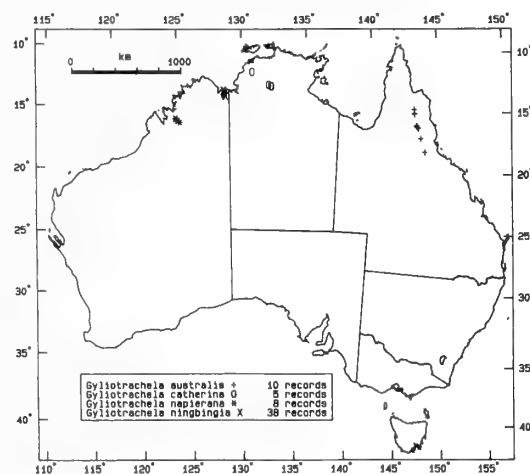


Figure 17

Ranges of *Gylotrachela australis*, *G. catherina*, *G. napierana*, and *G. ningbingia* in Australia.

The interior basins of Western Australia, southwest interior Queensland, and far north of South Australia below the Everard to Tomkinson Ranges are malacologically unexplored and quite probably nearly "snail-free" territory. At most one can expect to find scattered relict colonies. In contrast, the many Flinders Ranges and Eyre Highway associated records reflect both local abundance and many visits by collectors.

The above caveats should be kept in mind during all of the following discussions.

Generic and Species Ranges

A brief discussion of extralimital distributions precedes the description of Australian ranges. The generic sequence follows that of Table 2.

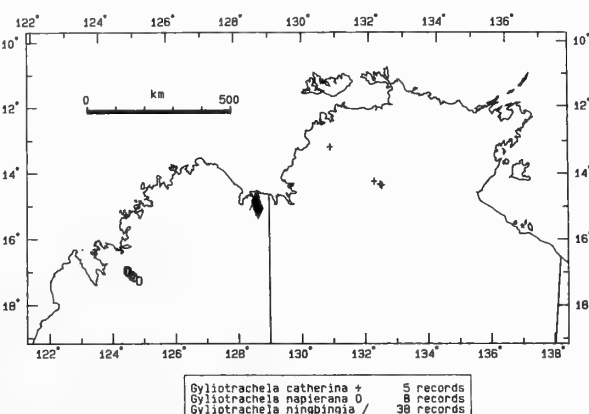


Figure 18

Records of *Gylotrachela catherina*, *G. napierana*, and *G. ningbingia* in the Kimberley and "Top End."

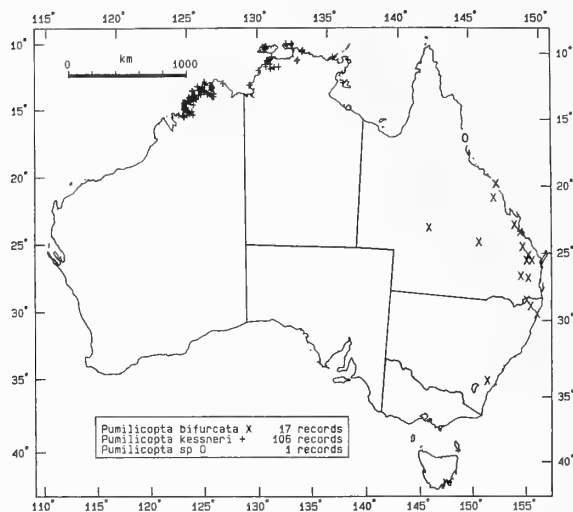


Figure 19

Ranges of *Pumilicopta bifurcata*, *P. kessneri*, and *Pumilicopta* sp. in Australia.

Nesopupa Pilsbry, 1900, according to the latest world monograph (PILSBRY, 1918–1920:270), has “Distribution: islands of the Pacific, Oriental, and Ethiopian regions, St. Helena. . . . Inhabiting widely separated island groups, there have been several nearly independent centers of evolution, making the construction of a phylogenetic classification exceptionally difficult.” There are two, possibly three, species in northern Australia. *Nesopupa mooreana* (Figure 2) is very common in the wetter areas of the Kimberley, reaching south to the tip of Dampierland, and was described from Roebuck Bay, near Broome. It is much less common in the “Top End” of the Northern Territory. *Nesopupa novopommerana* I. Rensch, 1932 (Figure 3) has been collected near Darwin at a few stations in the Drysdale River National Park in the Kimberley. Extraliminally, it lives in the Tanimbar Islands and Bismarck Archipelago. An as yet unidentified *Nesopupa* has been found

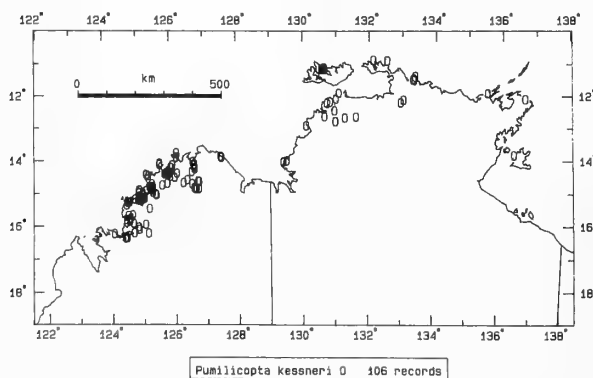


Figure 20

Records of *Pumilicopta kessneri* in the Kimberley and “Top End.”

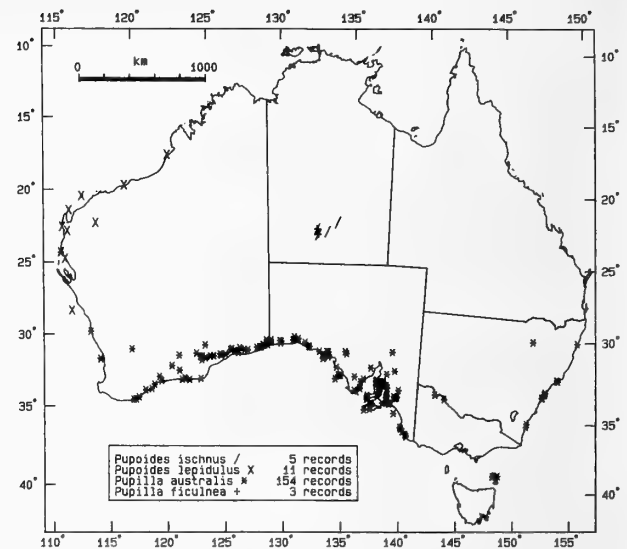


Figure 21

Ranges of *Pupilla australis*, *Pupilla ficulnea*, *Pupoides ischnus*, and *Pupoides lepidulus* in Australia.

in Gulf of Carpentaria and Cape York Peninsula collections, establishing a transnorthern Australia distribution for the genus *Nesopupa*.

Pupisoma Stoliczka, 1873, has about 18 species “in tropical and subtropical regions of both hemispheres except in arid districts and oceanic islands” (PILSBRY, 1920–1921: 19). Both *P. orcula* (Benson, 1850) (Figure 4) and *P. circumlitum* Hedley, 1897 (Figure 5) are common in wet areas from Dampierland across the top of Australia to

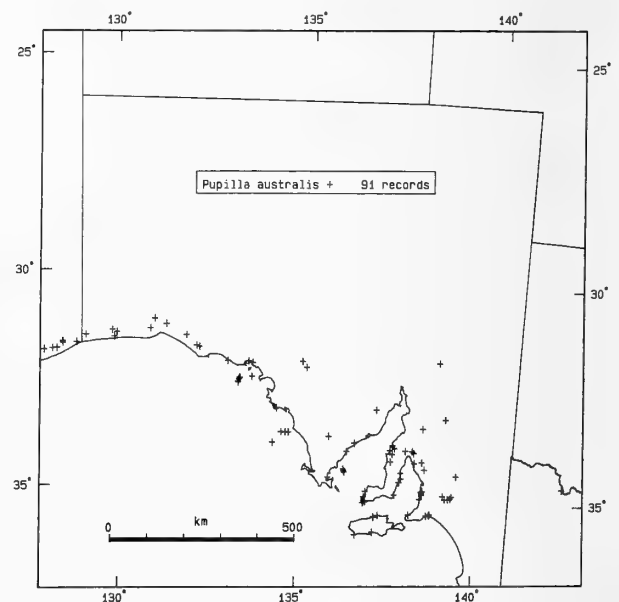


Figure 22

Records of *Pupilla australis* in South Australia.

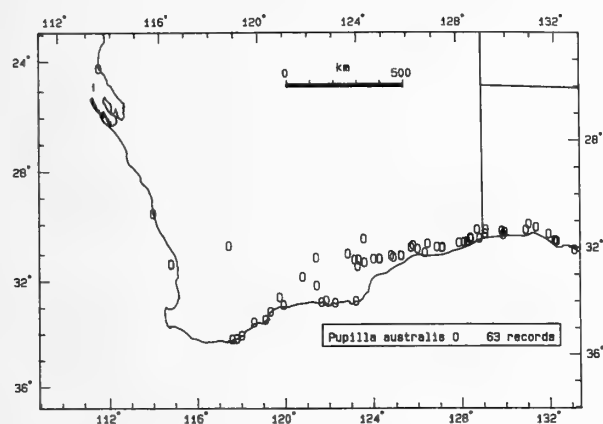


Figure 23

Records of *Pupilla australis* in southern Western Australia.

Torres Strait and northern Queensland, with the former much more abundant. They are conspicuously absent from the drier plains areas. An undescribed species, *Pupisoma* sp. (Figure 5), has been found near Katherine and on Goulburn Island in the Northern Territory, plus the Ningbing Ranges, east Kimberley. Controversy still exists as to whether the New World *P. dioscoricola* (C. B. Adams, 1845) and the Old World *P. orcula* are identical or not. A high degree of accidental transport by man has been hypothesized for *Pupisoma*, but the many rain-forest records in northern Australia strongly suggest natural occurrences. *Pupisoma* is a second transnorthern Australia genus.

Cylindrovertilla O. Boettger, 1880, has not been revised since PILSBRY (1920–1921:43–49). Less than five species have been recorded from New Caledonia, south Queens-

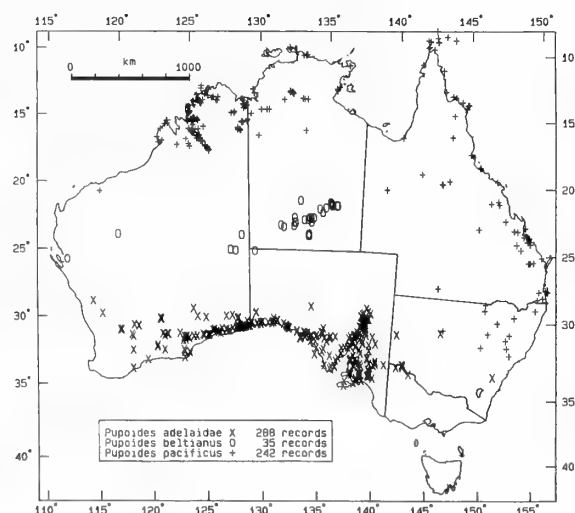


Figure 25

Records of *Pupoides adelaidae*, *P. beltianus*, and *P. pacificus* in Australia.

land, and New South Wales. The limits of distribution and the actual number of species are equally uncertain.

Gastrocopta probably has the widest natural range of any land snail genus, being "nearly world-wide in tropical and temperate regions, but wanting on many oceanic islands and in the recent European fauna, though represented there as Oligocene to Pliocene fossils" (PILSBRY, 1948:871). A few species have been widely disseminated by man, and two of these have reached Australia. *Gastrocopta servilis* (Gould, 1843), originally from the West Indies, has been collected near Broome and in Queensland;

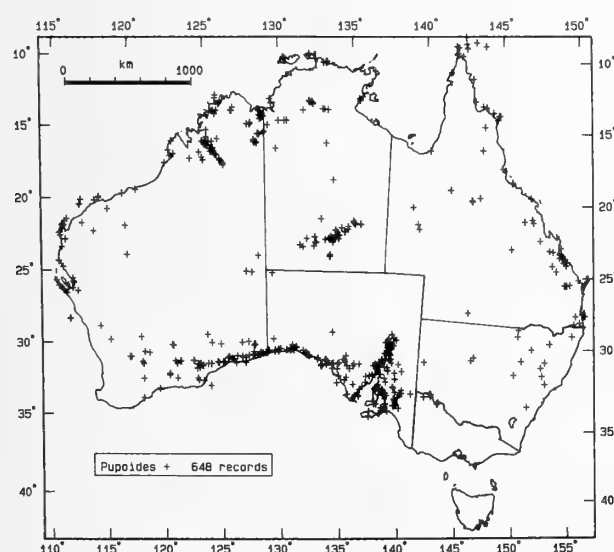


Figure 24

Records of *Pupoides* in Australia.

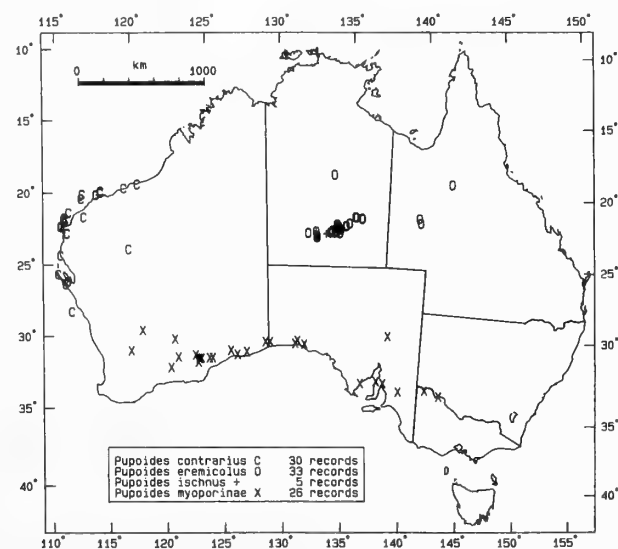


Figure 26

Records of *Pupoides contrarius*, *P. eremicolus*, *P. ischnus*, and *P. myoporinae* in Australia.

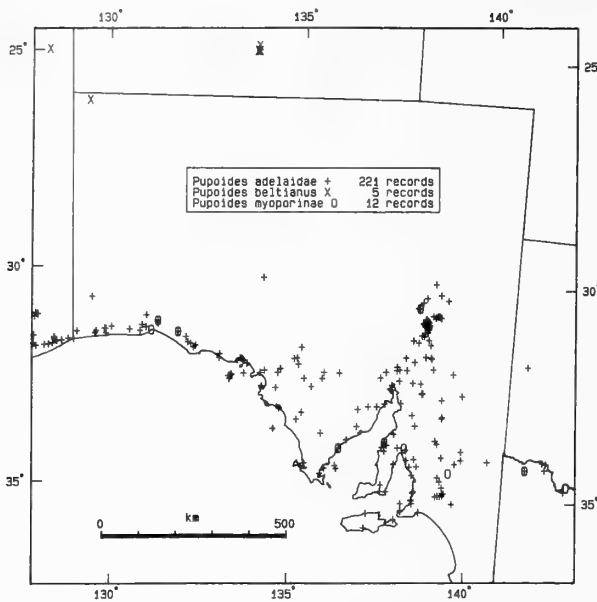


Figure 27

Records of *Pupoides adelaidae*, *P. beltianus*, and *P. myoporinae* in South Australia.

although listed under a variety of names, it is a common introduced species of New Guinea, Indonesia, and on many Pacific Islands (SOLEM, 1989:483–484). *Gastrocopta pediculus* is the most common Pacific Island species and has been present in Queensland and New South Wales for more than a century, again recorded previously under various names (SOLEM, 1989:486–487).

Gastrocopta is the most speciose of the Australian pupiloid genera, with 11 recognized species, plus two eastern states species, *G. strangeana* and *G. hedleyi*, that have not been revised. Extensive collections from the Gulf of Carpentaria and Cape York Peninsula remain to be studied. Probably additional species will be recognized.

Except for the humid southern areas (Figure 6), *Gastrocopta* is found throughout Australia. *Gastrocopta margaretae* (Cox, 1868) (Figure 7) is basically south coast; *G. deserti* (Figure 7) is "Red Centre" and western Queensland, but meets *G. margaretae* in the Flinders Ranges of South Australia (Figure 8), *G. pilbarana* Solem, 1986 on the west coast (Figure 9), and *G. simplex* Solem, 1989 (Figure 10) in the Kimberley. There are no other southern species. The "Red Centre" has *G. larapinta* (Tate, 1896) and *G. tatei* Pilsbry, 1917 (Figure 11), both of which have a few "dry fringe" records in the Kimberley and "Top End." The west coast has two species of relatively limited ranges, *G. pilbarana* and *G. wallabyensis* (E. A. Smith, 1894) (Figures 9, 12–15). Finally, there are a number of Kimberley-"Top End" species. *Gastrocopta simplex* (Figures 7, 10) is widely distributed; *G. mussoni* Pilsbry, 1917 (Figures 10, 32) lives on the desert fringes of the southwest Kimberley and also has been recorded from Mt. Morgan, Queensland; *G. macdonnelli* (Brazier, 1875) (Figure 16)

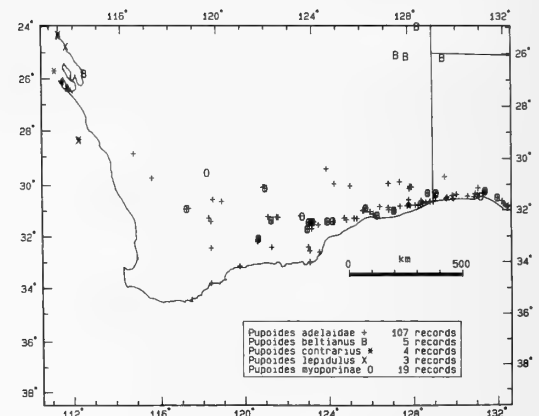


Figure 28

Records of *Pupoides adelaidae*, *P. beltianus*, *P. contrarius*, *P. lepidulus*, and *P. myoporinae* in southern Western Australia.

lives in coastal areas of the "Top End" and then ranges east to Torres Strait and northern Queensland; *G. macrodon* Pilsbry, 1917 (Figure 16) is restricted to wetter areas of the Kimberley, then recurs in the Louisiade Archipelago and Milne Bay, Papua; and *G. recondita* (Tapparone-Canefri, 1883) (Figure 16) lives in dryer portions of the south Kimberley and "Top End," with an extralimital extension to the Aru and Tanimbar Islands, plus Haruku near Ambon in the Moluccas. The range of *Gastrocopta* thus covers most of Australia.

Gyliotrachela ranges from Burma and Malaya through Indonesia to Timorlaut and the Tanimbar Islands, with a small radiation of four widely separated species in northern Australia (Figures 17, 18). All species are strictly limestone associated. The "Top End"-Kimberley taxa are from drier fringes. *Gyliotrachela* thus has an interrupted north Australian distribution, mainly from inland dry areas.

Pumilicopta Solem, 1989, has species on Sumba and Timor, plus *P. kessneri* Solem, 1989, in wet areas of the Kimberley and "Top End," an undescribed species from the Bellenden Ker Ranges, and *P. bifurcata* Solem, 1989, from scattered areas in Queensland and New South Wales (Figures 19, 20). Additional taxa have been collected recently in Cape York and Gulf of Carpentaria regions, thus giving *Pumilicopta* a transnorthern Australian and eastern states range.

Pupilla Leach, 1828, known from various parts of "North America, Eurasia, Africa, Australia, almost wholly in temperate and cold regions . . . is a widely distributed group, nowhere numerous in species, but generally abundant in individuals" (PILSBRY, 1948:927). The two Australian species have very different ranges. *Pupilla australis* (Adams & Angas, 1864) (Figures 21–23) has a south coast range with isolated records as far north as Carnarvon on the west coast; in the eastern states it reaches northern New South Wales and has been found on some islands in Bass Strait, Tasmania. *Pupilla ficulnea* (Tate, 1894) is a rare

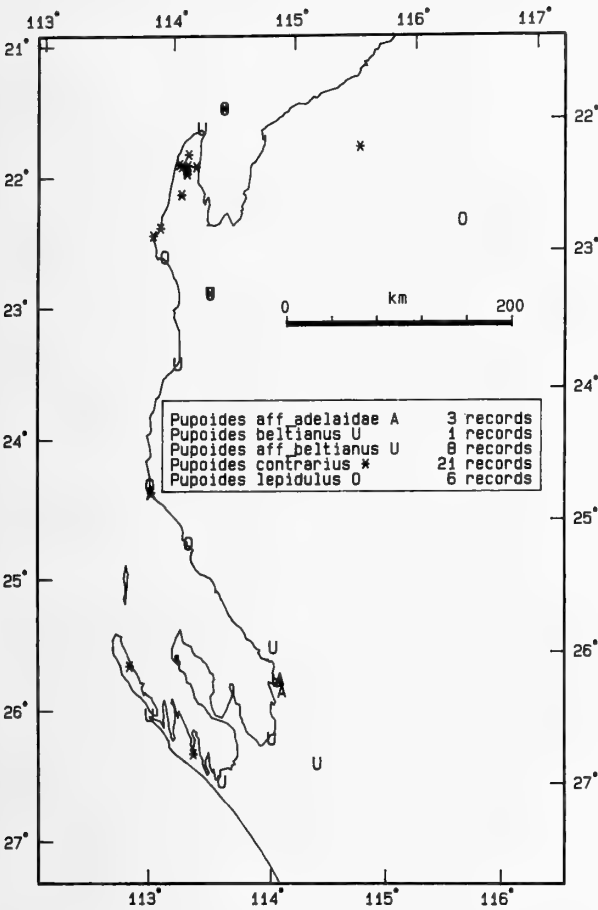


Figure 29

Records of *Pupoides* species and forms in the Shark Bay to North West Cape area of Western Australia.

species of limited range in the “Red Centre” (Figure 21). *Pupilla* thus has a southern range with an isolated species in the seasonally cold “Red Centre.”

Pupoides ranges within Australia as widely as *Gastrocopta* (compare Figures 6 and 24) and is the second most speciose genus of Australian pupilloids, with eight recognized species. Found on “all of the continents except Europe” (PILSBRY, 1948:920), “*Pupoides* is mainly a tropical and subtropical genus of arid regions or of relatively dry stations in humid areas. . . . The distribution of *Pupoides* is remarkably discontinuous . . . [and] the absence of the genus in southeastern Asia and East Indies [= Indonesia] leaves the Australian herd profoundly isolated” (PILSBRY, 1920–1921:109). *Pupoides pacificus* (Pfeiffer, 1846) (Figure 25) has a continuous range of Dampierland to Torres Strait and well into New South Wales (many additional Cape York and Gulf of Carpentaria collections were made in 1988). *Pupoides beltianus* (Tate, 1894) (Figure 25) has a “Red Centre” to Shark Bay range. *Pupoides adalaidae* (Adams & Angas, 1864) (Figure 25) is very common between Morawa (northeast of Perth, Western

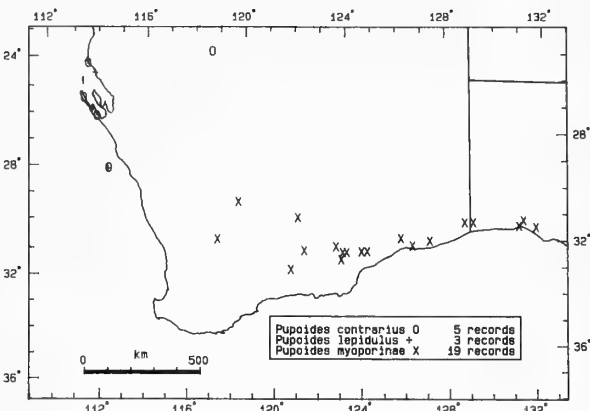


Figure 30

Records of *Pupoides contrarius*, *P. lepidulus*, and *P. myoporinae* in southern Western Australia.

Australia) to the Murray River, Victoria. *Pupoides eremicolus* (Tate, 1894) (Figure 26) is a “Red Centre” and western Queensland species. *Pupoides myoporinae* (Tate, 1880) (Figure 26) is a second south coast species, but less common than *P. adalaidae* and with a shorter range. *Pupoides lepidulus* (Adams & Angas, 1864) (Figure 21) and *P. contrarius* (E. A. Smith, 1894) (Figure 26) both have central west coast ranges in Western Australia. Finally, *P. ischnus* (Tate, 1894) (Figures 21, 26) is a rare species of the “Red Centre.”

A notable aspect of distribution in *Pupoides* is that whenever species ranges overlap, a dextrally coiled and a sinistrally coiled species are involved. The sympatric pairs are:

Area	Dextral species	Sinistral species
South coast	<i>adalaidae</i>	<i>Myoporinae</i>
West coast	<i>lepidulus</i>	<i>contrarius</i>
“Red Centre”	<i>beltianus</i>	<i>eremicolus</i> & <i>ischnus</i>

The only exception concerns *P. pacificus*, a dextral species, and the only *Pupoides* found in northern Australia and the eastern states. One sinistral population of a *Pupoides* was collected on Cassini Island, Admiralty Gulf, Kimberley in the 1890s (PILSBRY, 1920–1921:144), and it was collected again in 1988. Referred to as “form *sinistralis*” by Pilsbry, its taxonomic status remains to be determined.

Glyptopupoides is the only Australian restricted endemic genus. Originally considered to be a land prosobranch, the same species was redescribed by PILSBRY (1922–1926:252–253) and assigned to a new subgenus of *Pupoides*, which IREDALE (1937a:304) raised to generic rank in a checklist. *Glyptopupoides egregia* (Hedley & Musson, 1891) has a remarkable disjunct distribution, with one cluster of records from the fringes of inland rain-forest patches in the Kimberley (Figure 31), and an extended east coast range (Figure 32). Collecting in the Cape York area has marginally extended its range northwards. The disjunct Kimberley and Queensland-New South Wales range of *Glyp-*

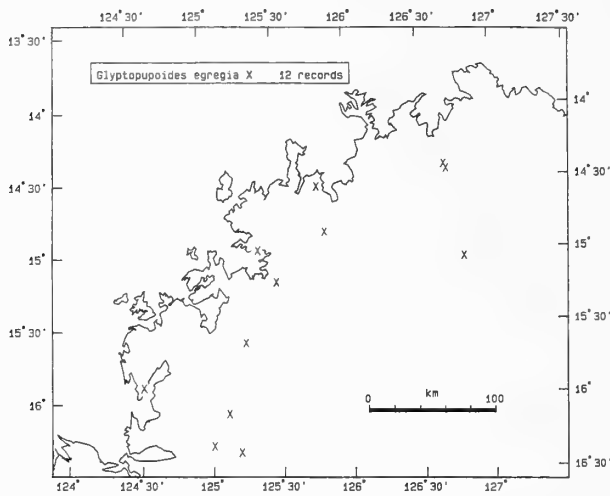


Figure 31

Records of *Glyptopupoides egregia* in the Kimberley and "Top End."

topupoides is nearly matched by that of *Gastrocopta mussoni* (Figure 32).

The nine genera thus have a few simple patterns of distribution:

(1) Only *Glyptopupoides* is a restricted endemic in Australia, showing a strikingly disjunct Kimberley and Queensland-New South Wales range (Figure 32);

(2) Two genera have regional extralimital ranges: *Cylindrovertilla* is found in New Caledonia and then the Queensland-New South Wales arc; and *Pumilicopta* has a Sumba and Timor range in Indonesia, followed by a continuous wetter forest range from the Kimberley to Torres Strait and into southern New South Wales (Figure 19);

(3) *Gyliotrachela* is characteristic of at least seasonally wet limestone areas from Burma through Indonesia, and has four isolated endemic species scattered across northern Australia (Figure 17);

(4) *Pupisoma* has a pantropical and pansubtropical distribution, some of which may be caused by accidental introduction on plants carried about by man—in Australia it has a wet forest transnorthern Australia range (Figures 4, 5);

(5) *Nesopupa* ranges from Africa and India to the furthest Pacific Islands, with limited wet forest northern Australian distribution (Figures 2, 3);

(6) *Pupilla* has a disjunct multicontinent distribution, with localized abundance, but not diversity, in temperate and colder regions, which fits its south coast and restricted "Red Centre" range in Australia (Figure 21); and

(7) Both *Gastrocopta* (Figure 6) and *Pupoides* (Figure 24) are nearly world-wide, but each has a few odd distributional gaps. Both genera are found throughout the pupilloid inhabitable parts of Australia, but not in Tasmania, most of Victoria, or the humid southwest corner of Western Australia.

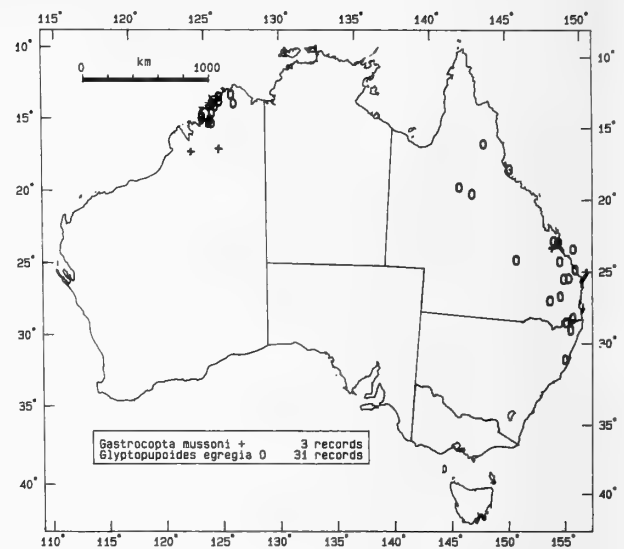


Figure 32

Ranges of *Gastrocopta mussoni* and *Glyptopupoides egregia* in Australia.

Regional Summary

On a regional basis, tropical northern Australia from the tip of Dampierland to Torres Strait and then south along the coastal forests of Queensland has the most diverse fauna, with: (1) *Pupisoma*, *Nesopupa*, *Pumilicopta*, *Gastrocopta*, and *Pupoides* ranging, at least in wetter areas, across the continent; (2) *Gyliotrachela* having a scattering of isolated species in seasonally dry limestone areas; and (3) *Glyptopupoides* showing a disjunct Kimberley, then Queensland-New South Wales range. Only the eastern *Cylindrovertilla* and the cool-temperate genus *Pupilla* are absent.

The at least seasonally wet eastern forests of Queensland and New South Wales, between the Great Dividing Range and the Pacific Ocean, have *Pupisoma*, *Nesopupa*, and one limited range species of *Gyliotrachela* in the north; *Glyptopupoides*, *Pupoides*, *Cylindrovertilla*, *Pumilicopta*, and a few *Gastrocopta* extending well to the south; and limited records of *Pupilla* extending north along mainly coastal New South Wales from its trans-Australian south coast range. Any given area may have fewer genera present than do the northern fringe sections, but the eastern wet forests include the whole range of pupilloid genera.

The south coast, from the New South Wales-South Australia border to Albany, Western Australia, has only three genera, *Gastrocopta*, *Pupoides*, and *Pupilla*. The "Red Centre" and the west coast of Western Australia from just south of Geraldton to Broome and Dampierland have the same limited group of genera present. Thus, the southern half of Australia, except for a limited extension south in the humid forests of New South Wales, has only three of the nine pupilloid genera.

Patterns of species diversity are similar. Four northern

Table 3
Species distribution patterns.

NORTHERN AUSTRALIA
Wet and intermediate areas (moving west to east)
Trans-Australia
<i>Pupisoma orcula</i>
<i>Pupisoma circumlitum</i>
<i>Pupoides pacificus</i>
Kimberley only
<i>Gastrocopta macrodon</i>
<i>Glyptopupoides egregia</i> (also QLD and NSW)
Kimberley and "Top End"
<i>Nesopupa mooreana</i>
<i>Nesopupa novopommerana</i>
<i>Pumilicopta kessneri</i>
<i>Pupisoma</i> sp.
"Top End" and Queensland
<i>Gastrocopta macdonnelli</i>
Queensland
<i>Pumilicopta</i> sp.
<i>Gyliotrachela australis</i>
<i>Pupisoma orcula</i> (from trans-Australia)
<i>Pupisoma circumlitum</i> (from trans-Australia)
<i>Gastrocopta mussoni</i> (from dry Kimberley)
unrevised <i>Gastrocopta</i> and <i>Pumilicopta</i>
Queensland-New South Wales
<i>Pumilicopta bifurcata</i>
<i>Gastrocopta strangeana</i>
<i>Gastrocopta hedleyi</i>
<i>Cylindrovertilla</i> spp.
<i>Pupoides pacificus</i> (from trans-Australia)
<i>Glyptopupoides egregia</i> (also Kimberley)
Dry fringes (moving west to east)
Kimberley
<i>Gastrocopta mussoni</i> (also S QLD)
<i>Gastrocopta larapinta</i> (from "Red Centre")
<i>Gastrocopta deserti</i> (from "Red Centre")
<i>Gyliotrachela napierana</i>
<i>Gyliotrachela ningbingia</i>
Kimberley and "Top End"
<i>Gastrocopta simplex</i>
<i>Gastrocopta recondita</i>
<i>Gastrocopta deserti</i> (from "Red Centre")
"Top End" only
<i>Gastrocopta tatei</i> (from "Red Centre")
<i>Gyliotrachela catherina</i>
Queensland
<i>Gastrocopta deserti</i> (from "Red Centre")
Kimberley and Queensland disjunct
<i>Gastrocopta mussoni</i>
<i>Glyptopupoides egregia</i>
"RED CENTRE"
<i>Gastrocopta deserti</i>
<i>Gastrocopta tatei</i>
<i>Gastrocopta larapinta</i>

Table 3
Continued.

<i>Pupoides beltianus</i>
<i>Pupoides eremicolus</i>
<i>Pupoides ischnus</i> (limited range)
<i>Pupilla ficulnea</i> (limited range)
WEST COAST AND PILBARA
<i>Gastrocopta deserti</i> (from "Red Centre")
<i>Gastrocopta pilbarana</i>
<i>Gastrocopta wallabyensis</i>
<i>Pupoides contrarius</i>
<i>Pupoides lepidulus</i>
SOUTH COAST AND FLINDERS
<i>Gastrocopta deserti</i> (from "Red Centre")
<i>Gastrocopta margaretae</i>
<i>Pupilla australis</i>
<i>Pupoides adelaidae</i>
<i>Pupoides myoporinae</i>

Australian species have extralimital ranges. *Pupisoma orcula* extends at least to southeast Asia and may be circumtropical; *Nesopupa novopommerana* has been collected on the Tanimbar Islands and New Britain, Bismarck Archipelago; *Gastrocopta macrodon* is restricted to the wet Kimberley, but then appears at Milne Bay, Papua, and in the Louisiade Archipelago; and *G. recondita*, from the dry south fringes of the Kimberley and "Top End," also lives in the Aru and Tanimbar Islands plus on Haruku near Ambon in the Moluccas, Indonesia.

Only two species show notable disjunctions within Australia. *Gastrocopta mussoni* has been recorded from two localities in the desert fringes of the south Kimberley and also from Mt. Morgan, Queensland. *Glyptopupoides egregia* has a fairly wide distribution on the fringes of mainly inland rain-forest patches in the Kimberley and an extensive Queensland-New South Wales range.

The general patterns of species distributions are summarized in Table 3. Nineteen of the 32 named species are present in some part of the Kimberley and "Top End," with a distinct difference between the dry fringes and the northern wetter zones. In contrast, the "Red Centre" has only seven species. The south coast and west coast each have four endemics plus an intrusion of *Gastrocopta deserti* from the "Red Centre." Data are inadequate to characterize the pupilloid fauna from the wet forests of Queensland and New South Wales, although that fauna is generically diverse and with at least a modest species radiation.

LOCAL DIVERSITY PATTERNS

Although recent collections from the Gulf of Carpentaria fringes and Cape York region have filled in a major collecting gap and provided many sympatric records, data from that survey are not available for interpretation at this time. Historic records from the literature cannot be depended upon for an accurate depiction of sympatry, and

Table 4
Pupilloid species in Kimberley wet areas.

Species	Island samples (n = 91)		Coastal samples (n = 35)		Inland samples (n = 31)	
	Number	Percent	Number	Percent	Number	Percent
<i>Gastrocopta macrodon</i>	74	81.3	27	77.1	20	64.5
<i>Gastrocopta simplex</i>	9	9.9	1	2.9	5	16.1
<i>Glyptopupoides egregia</i>	2	2.2	2	5.7	8	25.8
<i>Nesopupa mooreana</i>	48	52.7	28	80.0	20	64.5
<i>Pupisoma circumlitum</i>	9	9.9	3	8.6	10	32.3
<i>Pupisoma orcula</i>	32	35.2	25	71.4	23	74.2
<i>Pupoides pacificus</i>	26	28.6	12	34.3	12	38.7
<i>Pumilicopta kessneri</i>	38	41.8	34	97.1	18	58.1

thus comments on the Queensland-New South Wales patterns must be deferred. Preliminary review of the new collections suggests that local diversity rarely reaches four species and that distribution is patchier than in the Kimberley.

Both the south and west coasts of Australia have a limited fauna (Table 3). Both areas have fringe records of the "Red Centre" species *Gastrocopta deserti* (Figures 8, 9, 14, 15), sometimes involving microsympatry with other *Gastrocopta*. The south coast has four species with rather wide ranges: (1) *Pupilla australis* (Figure 21) is more coastal and extends to the coast of New South Wales; (2) *Gastrocopta margaretae* (Fig. 7) inhabits much of the Flinders Ranges, but does not extend as far east or west as does *Pupilla australis*; (3) *Pupoides adelaidae* (Figure 25) extends further inland and westward; and (4) *Pupoides myoporinae* (Figure 26), which is much less abundant, has a less extensive range, and is absent from much of the Eyre Peninsula. The two species of *Pupoides* show occasional sympatry in South Australia (Figure 27), but *P. adelaidae* is much more abundant and widely distributed. In Western Australia (Figure 28), most records of *P. myoporinae* involve sympatry with *P. adelaidae*. In coastal and Eyre Highway sections, sympatry of all four species is not unusual, with inland records showing loss of the more coastal taxa. *Pupilla australis* (Figures 22, 23) has inland records in South Australia but mainly coastal records in Western Australia.

Interpretation of west coast records is premature, because many collections consist only of sifted drift material, and thus potentially represent mixed habitat information. Records are few in number, reflecting both the harsh habitat and the comparatively limited collecting done in this region. From Shark Bay to just north of the North West Cape, there are four *Pupoides* (Figure 29) recognized (see SOLEM, 1986:107–115): *Pupoides lepidulus* (Figure 21) and *P. contrarius* (Figure 26), both restricted endemics; an apparent intrusion of the "Red Centre" species *P. beltianus* (Figure 25); and a very few records of the south coast *P. adelaidae*. The endemics (Figures 28, 30) often are microsympatric. The otherwise southern species *Pupilla australis* (Figure 23) is known from a single record at Point Quobba,

north of Carnarvon. *Gastrocopta* is represented by a few species. Several records are known for the "Red Centre" species *G. deserti* (Figures 9, 14, 15); and two endemic species, *G. wallabyensis* and *G. pilbarana* (Figures 13–15), have limited records, with occasional microsympatry. Much more collecting is needed in this region.

The "Red Centre" has a slightly more extensive radiation, showing a mixture of very common and widely distributed species (*Gastrocopta deserti*, Figure 7; *Pupoides beltianus*, Figure 25; *P. eremicolus*, Figure 26), widely distributed, but clearly disjunct taxa (*G. tatei*, Figures 11, 12; *G. larapinta*, Figure 11), and two species of very limited "Red Centre" distribution (*Pupilla ficulnea*, Figure 21; *Pupoides ischnus*, Figures 12, 21).

All of the species have been collected from stream drift or fig litter near Glen Helen (WA-113), MacDonnell Ranges, and in Palm Valley (WA-130, WA-131), Krichauff Ranges. All of these localities lie in the Finke River drainage. The relative abundance of the three species of *Gastrocopta* varies greatly from locality to locality (SOLEM, 1989:490). Once the wetter mountains are left, the number of microsympatric species declines. *Pupilla ficulnea* and *Pupoides ischnus* are restricted to the central area (Figure 21). The dextral species *Pupoides beltianus* (Figure 25) is common from the Jervois Range, northeast of Alice Springs, to the Barrow Range in Western Australia, with a probable extension to the Shark Bay area (Figure 29). The sinistral *Pupoides eremicolus* (Figure 26) has been collected at Boulia, Black Mt., and Saxby Downs Homestead in western Queensland, then from Tennant Creek and the Dulcie Range through the Krichauff Ranges; it has not been collected in Western Australia. *Gastrocopta deserti* (Figure 7) has a significant set of western Queensland records, inhabits northern parts of the Flinders Ranges, where it has one microsympatric record with *G. margaretae* (Figure 8), is common in the Everard and Mann Ranges (Figure 8), reaches the south fringes of the Kimberley, and near Katherine in the Northern Territory (Figure 10), and then the west coast between Point Quobba and Dampierland (Figures 9, 14, 15). *Gastrocopta tatei* (Figure 11) partly overlaps the range of *G. larapinta* in the "Red Centre," but extends farther west and has an isolated

Table 5
Species diversity in Kimberley wet areas.

Number of species	Island samples		Coastal samples		Inland samples	
	Number	Percent	Number	Percent	Number	Percent
0	10	11.0	0	0.0	2	6.5
1	20	22.0	2	5.7	2	6.5
2	14	15.4	2	5.7	3	9.7
3	18	19.8	11	31.4	4	12.9
4	14	15.4	12	34.5	8	25.8
5	10	11.0	6	17.1	8	25.8
6	5	5.5	1	2.9	4	12.9
7	0	0.0	1	2.9	0	0.0
TOTALS	91	100.1	35	100.0	31	100.0
Mean number of species/sample	2.62		3.74		3.74	

record near Elsey Falls, Roper River, "Top End." *Gastrocopta larapinta* extends farther east into the Dulcie and Jervois Ranges (Figure 11) and then appears in Brooking Gorge, Oscar Ranges, Western Australia, plus a more northern locality, the Carson Escarpment.

Thus, only two species, *Pupoides ischnus* and *Pupilla ficulnea*, are restricted to the "Red Centre." The other five show varying patterns of presence in other parts of Australia.

In wetter refugia of the "Red Centre," most pupilloid species can be found in the litter under a single small patch of figs.

The Kimberley and "Top End" have the largest number of species and the most complex patterns of local diversity. A basic area differentiation must be made on moisture patterns. The Darwin to Gulf of Carpentaria part of the "Top End" and the Prince Regent River to Kalumburu part of the northwest Kimberley have 1000–1500 mm wet seasons. The area near Katherine, Northern Territory, the area along the border from Sir Joseph Bonaparte Gulf inland to Halls Creek, and the chain of Devonian limestone reefs from the Napier Range southeast through the Emanuel and Lawford Ranges have only a 500–759 mm wet season. The two coastal and slightly inland wet regions thus grade into drier and eventually inland desert regions to the south. In addition, they are separated by a trough of land with reduced rainfall that extends along the Western Australia-Northern Territory (WA-NT) border. Each section of this region has its own peculiarities of faunal composition and diversity patterns. Distributional data on the "Top End" sections are based upon several sources: collections made by Vince Kessner, as reported in SOLEM (1989:468–516); collections from the "dry trough of the WA-NT border area" made by the author and reported on in SOLEM (1988:71–74); collections from the limestone fringes of the south Kimberley by A. Solem in 1976–1985 and R. Cameron in 1988; and the Kimberley wet area collections primarily by Vince Kessner during the Rain-

forest Survey of June 1987 (reported on in SOLEM, in press) and the Kimberley Coast Expedition of June and July 1988 (data summarized here).

Fringe intruders from other regions number seven: *Nesopupa novopommerana* (Figure 3) from near Darwin and the Drysdale River, then Tanimbar Islands and New Britain, Bismarck Archipelago; *Gastrocopta macdonnelli* (Figures 11, 16) from Darwin and Melville Island east to Torres Strait and south at least to Townsville, Queensland; *Gastrocopta deserti*, *G. tatei*, and *G. larapinta*, all from the "Red Centre" (Figures 10, 11); *Gastrocopta mussoni* (Figures 3, 32), described from near coastal Queensland; and *Glyptopupoides egregia* (Figures 31, 32) from Queensland and northern New South Wales, and then mainly inland parts of the Kimberley wet area.

The wet portion of the "Top End" has a typical assemblage of *Pupisoma orcula*, *Pupisoma circumlitum*, *Pumiliocopta kessneri*, *Nesopupa mooreana*, and *Gastrocopta macdonnelli* (near the coast) or *G. simplex* (more inland). Dry inland areas will tend to have *Gastrocopta recondita* (otherwise an Indonesian species), *Pupoides pacificus*, *G. simplex* (or *G. deserti*, *G. tatei*, etc.), and (on limestone) *Gyliotrachela catherina*, but will be without some of the wetter area taxa. There thus is a common pattern of three to five microsympatric species.

The zone along the WA-NT border has many limestone hills that, in general, hold large land snail populations. In the wetter northern area of the Ningbing Ranges and Jeremiah Hills, the restricted endemic *Gyliotrachela ningbingia* (Figures 17, 18) and *Gastrocopta simplex* (Figures 7, 10) are nearly ubiquitous (see SOLEM, 1988:90, 94), while *Pupoides pacificus* (Figure 25; SOLEM, 1988:97) is much less common. There are one to three records each for *Pupisoma orcula*, *Pupisoma* sp., and *Nesopupa mooreana* from swamp adjacent to the Ningbing Ranges. Further inland, there are only records of *Gastrocopta simplex*, *Pupoides pacificus*, and occasionally *G. deserti* or *G. recondita*. A pattern of two or three microsympatric species is typical.

Along the limestone hills that border the south margin of the Kimberley, there is a clear pattern of gradual reduction in species diversity from the wetter northwest corner (750 mm) to the much drier Lawford Ranges (550 mm). Rainfall records are not adequate to provide correlations, but the general pattern is simple. In the northwest Napiers, *Gastrocopta macrodon* (a wet Kimberley taxon at its southern limit), *G. recondita* (a south fringes species at its northern Australian limit), sometimes *G. simplex* (a dry Kimberley-"Top End" species), *Pupoides pacificus* (a dry zone transcontinental north Australian species), and *Gyliotrachela napierana* (Figures 17, 18; a restricted endemic in the northwest Napier Range) can be present. This gives a four to five microsympatric species pattern. *Gastrocopta macrodon* has a sporadic range, from the Van Emmerick Range to Stumpy's Well, then reappearing about 2-4.7 km south of Yammera Gap, and again near the Lillimilura Police Station ruins. *Gastrocopta recondita* and *Pupoides pacificus* continue throughout the limestone hills, and *Gastrocopta simplex* becomes more abundant to the southeast. *Gyliotrachela napierana* extends southeast to Barker Gorge and then reappears briefly in a highly dissected set of hills about 2.3-2.4 km south of Wombarella Gap and at the "Dingo Caves" some 10.6 km south of Yammera Gap. From here to Brooking Gorge in the Oscar Ranges, the number of pupilloid species is usually only two or three—*Gastrocopta recondita* and/or *G. simplex*, and *Pupoides pacificus*. In Brooking Gorge, there are isolated records for *Gastrocopta larapinta*, and *G. mussoni* has been collected near the Brooking Spring Station air strip, increasing the degree of local diversity. Southeast of the Oscar Range, there are only scattered records for *G. simplex* and *P. pacificus*.

Thus, diversity along the south fringe of the Kimberley shifts from five to two species along a northwest to southeast axis. This correlates with a similar gradient of decrease in wet season rainfall.

The greatest numbers of species and genera, plus the highest levels of local diversity, are found in the wet areas of the northwest Kimberley (see Tables 4, 5). Two comprehensive field surveys provided directly comparable data on local diversity in relation to habitat and area history, permitting observations on local diversity shifts. The Rainforest Survey of June 1987 focused on a broad sampling of vine thicket patches throughout the Kimberley, making 82 stations in 20 field days. Their sampling included very few stations from islands, because the helicopter used in this survey was not equipped with over-water safety equipment. In June and July 1988, a joint Western Australian Museum-Australian Museum-Field Museum of Natural History expedition visited 84 islands off the Kimberley Coast using the chartered vessel *North Star* and made 115 collecting stations. A very few of the stations from the two trips overlapped.

Of the pupilloid species previously collected in the Kimberley and reported on by SOLEM (1989), only *Nesopupa novopommerana*, from inland portions of the Drysdale River National Park, was not obtained by the two survey teams. The only possibly additional species obtained were: (1) a small series of dead *Gastrocopta* from near Kalumburu (SOLEM, in press) that may represent an unknown species or may be subadults of a known species and (2) a recollected, sinistral *Pupoides* from Cassini Island that probably is distinct.

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APPENDIX 1

List of Reviewed Australian Pupilloid Taxa

* Indicates an introduced species.

Genus *Gastrocopta* Wollaston, 1878

(Synonyms: *Australbinula* Pilsbry, 1916; *Gyrodaria* Iredale, 1940;

Papualbinula Iredale, 1941)

Gastrocopta deserti Pilsbry, 1917

Synonym: *helmsiana* Iredale, 1939.

See SOLEM, 1986:102–103, figs. 13–15; SOLEM, 1989: 487–489, figs. 48–53.

Type locality: "Red Centre," Australia.

Gastrocopta larapinta (Tate, 1896)

See SOLEM, 1989:490–491, figs. 54–55.

Type locality: "Red Centre," Australia.

Gastrocopta macdonnelli (Brazier, 1875)

See SOLEM, 1989:492–493, figs. 60–61.

Type locality: Fitzroy Island, NE Queensland.

Gastrocopta macrodon Pilsbry, 1917

See SOLEM, 1989:495–496, figs. 62–67.

Type locality: Milne Bay, Papua, New Guinea.

Gastrocopta margaretae (Cox, 1868)

Synonyms: *bannertonensis* Gabriel, 1930; *complexa* Iredale, 1939.

See SOLEM, 1986:99–101, figs. 1–10.

Type locality: Wallaroo, South Australia.

Gastrocopta mussoni Pilsbry, 1917

See SOLEM, 1989:494, figs. 211–213.

Type locality: Calliungal (= Mt. Morgan), SE Queensland.

**Gastrocopta pediculus* (Shuttleworth, 1852)

See SOLEM, 1989:486–487, figs. 46–47.

Type locality: Marquesas Islands.

Comment: Probably of Indonesian origin.

Gastrocopta pilbarana Solem, 1986

See SOLEM, 1986:103–104, figs. 16–20.

Type locality: Sandy Point, Dirk Hartog Island, Shark Bay, Western Australia.

Gastrocopta recondita (Tapparone-Canefri, 1883)

Synonym: *niobe* Fulton, 1899.

See SOLEM, 1989:496–497, figs. 73–78.

Type locality: Wokan, Aru Islands.

**Gastrocopta servilis* (Gould, 1843)

Synonyms: *microsoma* Tapparone-Canefri, 1883; *lyonsiana* Ancey, 1892.

See SOLEM, 1989:483–484, figs. 38–41.

Type locality: near Matanzas, Cuba.

Comment: Of West Indian origin, introduced on plants.

Gastrocopta simplex Solem, 1989

See SOLEM, 1989:484–486, figs. 42–45.

Type locality: Pentecost River, El Questro Homestead, SW of Wyndham, Western Australia.

Gastrocopta tatei Pilsbry, 1917

See SOLEM, 1989:491–492, figs. 56–59.

Type locality: Central Australia.

Gastrocopta wallabyensis (E. A. Smith, 1894)

See SOLEM, 1986:101–102, figs. 11–12.

Type locality: E Wallaby Island, Houtman Abrolhos group, Western Australia.

Genus *Glyptopupoides* Pilsbry, 1926

(Synonym: *Famarinia* Iredale, 1933)

Glyptopupoides egregia (Hedley & Musson, 1891)

Synonym: *hedleyi* Pilsbry, 1926.

See SOLEM, 1989:506–508, figs. 214–217.

Type locality: Calliungal (= Mt. Morgan), Queensland.

Genus *Gyliotrachela* Tomlin, 1930

(Synonyms: *Gyliauchen* Pilsbry, 1917 [*non* Nicoll, 1915];

Gyliotrachela Pilsbry, 1931)

Gyliotrachela australis (Odhner, 1917)

See SOLEM, 1981:92, figs. 7, 8, 12.

Type locality: Chillagoe Caves, N Queensland.

Gyliotrachela catherina Solem, 1981

See SOLEM, 1981:91–92, figs. 5, 6, 11, 17; SOLEM, 1989: 504–505, figs. 97–102.

Type locality: 19 km S of Katherine, Northern Territory.

Gyliotrachela napierana Solem, 1981

See SOLEM, 1981:91, figs. 3, 4, 10, 14–16, 18, 19; SOLEM, 1989:503–504, figs. 94–96.

Type locality: 5.7 km N of No. 8 Bore, Ningbing Ranges, N of Kununurra, Western Australia.

Genus *Nesopupa* Pilsbry, 1900

(Synonym: *Westralcopta* Iredale, 1939)

Nesopupa mooreana (E. A. Smith, 1894)

See SOLEM, 1989:477–479, figs. 33–37.

Type locality: Roebuck Bay, Western Australia.

Nesopupa novopommerana I. Rensch, 1932

Synonym: *tenimberica* Haas, 1937.

See SOLEM, 1989:476–477, figs. 27–32.

Type locality: Karlei, Weite Bucht, Neu-Pommern (= New Britain), Bismarck Archipelago.

Genus *Pumilicopta* Solem, 1989

Pumilicopta bifurcata Solem, 1989

See SOLEM, 1989:497–498, figs. 88–90.

Type locality: Mountain near Bouldercome, central Queensland.

Pumilicopta kessneri Solem, 1989

See SOLEM, 1989:499–500, figs. 85–87.

Type locality: Wunyu Beach, West Arnhem Land, Northern Territory.

Pumilicopta sp.

See SOLEM, 1989:498.

Locality: Westgid Creek, Bellenden Ker Range, north-east Queensland.

Genus *Pupilla* Leach, 1828(Synonym: *Omegapilla* Iredale, 1937)*Pupilla (Gibbulinopsis) australis* (Adams & Angas, 1864)Synonyms: *lincolniensis* Cox, 1867; *occidentalis* Iredale, 1939.

See SOLEM, 1986:105–107, figs. 21–24.

Type locality: Fleurieu Peninsula, South Australia.

Pupilla (Gibbulinopsis) ficulnea (Tate, 1894)

See SOLEM, 1989:505–506, figs. 103–104.

Type locality: Central Australia.

Genus *Pupisoma* Stoliczka, 1873(Synonym: *Imputegula* Iredale, 1937)*Pupisoma circumlitum* Hedley, 1897

See SOLEM, 1989:473–474, figs. 17, 24, 25.

Type locality: Bundaberg, Queensland.

Pupisoma orcula (Benson, 1850)

See SOLEM, 1989:472–473, figs. 18, 21–23.

Type locality: Between Jounpore and Benares, India.

Pupisoma sp.

See SOLEM, 1989:475, figs. 16, 26.

Locality: Scattered Northern Territory records and Ningbing Ranges, Western Australia.

Genus *Pupoides* Pfeiffer, 1854(Synonymy: *Themapupa* Iredale, 1930)*Pupoides adelaidae* (Adams & Angas, 1864)Synonyms: *ramsayi* Cox, 1864; *asserta* Iredale, 1939; *contexta* Iredale, 1939; *amolita* Iredale, 1940.

See SOLEM, 1986:111–113, fig. 31.

Type locality: South Australia.

Pupoides aff. *adelaidae* (Adams & Angas, 1864)

See SOLEM, 1986:114–115, figs. 32–33.

Locality: Shark Bay and slightly north, Western Australia.

Pupoides beltianus (Tate, 1894)

See SOLEM, 1989:511–513, fig. 107.

Type locality: Central Australia.

Pupoides aff. *beltianus* (Tate, 1894)

See SOLEM, 1986:114, fig. 36.

Locality: Shark Bay to North West Cape and Hamersley Range, Western Australia.

Pupoides contrarius (E. A. Smith, 1894)

See SOLEM, 1986:109–111, figs. 27, 28.

Type locality: East Wallaby Island, Houtman Abrolhos, Western Australia.

Pupoides eremicolus (Tate, 1894)

See SOLEM, 1989:509–511, fig. 106.

Type locality: Central Australia.

Pupoides ischnus (Tate, 1894)Synonym: *laticus* Iredale, 1937.

See SOLEM, 1989:508–509, fig. 105.

Type locality: Central Australia.

Pupoides lepidulus (Adams & Angas, 1864)

See SOLEM, 1986:113–114, fig. 34.

Type locality: Shark Bay, Western Australia.

Pupoides myoporinae (Tate, 1880)Synonym: *sinistrorsus* Tate, 1879 [non Serres, 1841].

See SOLEM, 1986:108–109, figs. 25, 26.

Type locality: Peelunbie, Head of the (Great Australian) Bight, South Australia.

Pupoides pacificus (Pfeiffer, 1846)Synonyms: *anapacifica* Iredale, 1939; *dirupta* Iredale, 1939; *comperta* Iredale, 1940.

See SOLEM, 1989:513–516, figs. 108–114.

Type locality: Sir Charles Hardy's Island, Cape York Peninsula, Queensland.

List of Unrevised Pupilloid Taxa

The following taxa listed in the nomenclatural checklist of IREDALE (1937a:301–306) have not been reviewed for lack of adequate material. It is possible neither to characterize them adequately as species nor to delineate meaningful distributional ranges. References are given both to IREDALE (1937a) and the early revisions by PILSBRY (1916–1918, 1920–1921). Comments are given where appropriate.

Gastrocopta hedleyi Pilsbry, 1917

See PILSBRY, 1916–1918:166–167, pl. 27, figs. 1–4; IREDALE, 1937a:301.

Type locality: Narrabri, New South Wales.

Comment: A dextral shell with a huge, slanted columellar barrier whose anterior end is lower; parietal long and crescentic; basal tiny and tubercular; lower palatal strongly angled.

Gastrocopta macleayi (Brazier, 1876)

See PILSBRY, 1916–1918:162–164, pl. 27, fig. 9; IREDALE, 1937a:302.

Type locality: Bet and Sue Islands, Torres Strait, Queensland.

Comment: Probably a synonym of *G. macdonnelli* (Brazier, 1875).

Gastrocopta moretonensis (Cox, 1868)

See PILSBRY, 1916–1918:161–162, pl. 26, figs. 12, 13; IREDALE, 1937a:301.

Type locality: Moreton Bay, Queensland.

Comment: Type specimens probably lost, no topotypes seen; original illustration inadequate for identification purposes.

Gastrocopta queenslandica Pilsbry, 1917

See PILSBRY, 1916–1918:159–160, pl. 26, fig. 2; IREDALE, 1937a:301.

Type locality: Calliungal (= Mt. Morgan), Queensland.

Comment: The type illustration looks like a "new adult" of *G. pediculus* (Shuttleworth, 1852) in which the apertural barriers are still undersized.

Gastrocopta rossiteri (Brazier, 1875)

See PILSBRY, 1916–1918:147; IREDALE, 1937a:302.

Type locality: Picton, New South Wales.

Comment: Probably based upon examples of *G. pediculus* (Shuttleworth, 1852).

Gastrocopta strangeana Iredale, 1937

Synonym: *strangei* Pfeiffer, 1854, non Benson, 1853.

See PILSBRY, 1916–1918:157–158, pl. 26, figs. 3–6; IREDALE, 1937a:301.

Type locality: Gordon (= Garden) Island, Port Jackson, New South Wales.

Comment: A sinistral shell with the parietal and angular barriers well separated; columellar barrier simple and not inclined; basal a tiny knob; lower palatal crescentic; upper palatal a medium-sized knob. The only sinistral Australian *Gastrocopta*. IREDALE (1940:234) proposed a new genus, *Gyrodaria*, for this species.

Gastrocopta strangeana trita (Iredale, 1940)

See IREDALE, 1940:233–234, fig. 3.

Type locality: Narrabri, New South Wales.

Comment: A "larger sinistral form" of *G. strangeana* is the only differentiating phrase. Probably a *nomen nudum*.

Genus *Cylindrovertilla* Boettger, 1880

(Synonym: *Wallivertilla* Iredale, 1937)

Comment: Minute, sinistral shells, recorded from New Caledonia and the Queensland-New South Wales arc; mainly coastal areas. Parietal barrier has been lost, but a prominent angular barrier remains.

Cylindrovertilla fabreana boynensis Iredale, 1937

See PILSBRY, 1916–1918:47–48, pl. 5, figs. 12, 13; IREDALE, 1937a:303.

Type locality: Boyne Island, Port Curtis, Queensland.

Cylindrovertilla hedleyi Pilsbry, 1920

See PILSBRY, 1920–1921:46, pl. 5, figs. 4, 10; IREDALE, 1937a:303.

Type locality: Calliungal (= Mt. Morgan), Queensland.

Comment: Lower palatal barrier lost, others reduced in size.

Cylindrovertilla kingi (Cox, 1864)

See PILSBRY, 1920–1921:44–46, pl. 5, figs. 1–3; IREDALE, 1937a:303.

Type locality: Paramatta, New South Wales.

Comment: Two palatal barriers present.

Cylindrovertilla kingi negata Iredale, 1940

See IREDALE, 1940:233, 235, fig. 2.

Type locality: Tweed River, New South Wales.

Comment: Probably a synonym of *C. kingi* (Cox, 1864).

Pupilla nelsoni (Cox, 1864)

See PILSBRY, 1920–1921:219–220—as synonym of *P. australis* [Adams & Angas, 1864]; also see IREDALE, 1937a:304.

Type locality: Nelson's Bay, Sydney, New South Wales.

Comment: Probably a synonym of *P. australis*.

Pupilla tasmanica (Johnston, 1883)

See PILSBRY, 1920–1921:219–221, pl. 23, fig. 18—as synonym of *P. australis* [Adams & Angas, 1864]; also see IREDALE, 1937a:305.

Type locality: Tasmania.

Comment: Probably a synonym of *P. australis*.

Genus *Somniopupa* Iredale, 1937

Comment: Quite probably a *nomen nudum*.

Somniopupa scotti Brazier, 1875

See PILSBRY, 1920–1921:222, pl. 23, fig. 22; IREDALE, 1937a:305.

Type locality: Fitzroy Island, Queensland.

Comment: Based on a single, probably juvenile example.

Very probably a synonym, but its identity remains uncertain.

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Terrestrial Snails (Gastropoda) in Dominican Amber

by

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Abstract. Seven species of land snails are reported from amber of late Oligocene (25 Ma) to late Eocene (40 Ma) age from the Dominican Republic: *Strobilops* (?*Coelostrobilops*) sp.; *Subulina* sp.; *Spiraxis* sp.; ?ferussaciid, genus and species indeterminate; *Varicella* sp.; helicimid, genus and species indeterminate; and a prosobranch land snail of indeterminate family. As far as determinable, all are within the modern geographic ranges of their taxonomic groups. The taxa are indicative of a tropical or paratropical climate. Strobilopsidae assignable to modern genera and subgenera may have been present in the American tropics at least as early as in western Europe.

INTRODUCTION

Fossil remains of terrestrial snails (Gastropoda: Pulmonata and Prosobranchia) in amber are relatively rare. Shells identified as species of *Electrea* (?Cyclophoridae), *Strobilus* (= *Strobilops*; Strobilopsidae), *Vertigo* (Pupillidae), *Balea* (Clausiliidae), *Hyalina* (= *Euconulus*; Euconulidae), *Microcystis* (Euconulidae), and *Parmacella* (Parmacellidae) have been reported from amber of the Baltic region (KLEBS, 1886; SANDBERGER, 1887; LARSSON, 1978; family names updated). Photographs of unidentified snails in amber from the Dominican Republic have been presented in popular books (SCHLEE, 1980, 1986). Those and the forms described here are at least late Oligocene (25 Ma) in age and may be as old as late Eocene (40 Ma); they represent the earliest records of fossil land snails in Mesoamerica. The specimens described in this paper were obtained by the senior author from private collections and commercial sources. They are well preserved, many with soft tissues present. All probably represent snails that were living at the time they became covered with resin. Several show gas bubbles, which may represent gaseous products of decomposition or perhaps the expulsion of mucous froth by the entrapped animals. Only their preservation in the middle of blocks of fossil resin precludes description of the species in full detail. The specimens document the presence of seven land snail families in this chronostratigraphic setting. Four of the specimens can be assigned to specific extant genera. In the case of *Strobilops*, the occurrence alters historical biogeographic hypotheses that have been proposed

for its group. All provide useful "tie points" for the ranges of their groups during the early to medial Tertiary period.

MATERIALS AND METHODS

The fossils in amber described here are from mines located in the Cordillera Septentrional of the Dominican Republic. The source is the Altamira facies of the El Mamey Formation, shale and sandstone interspersed with conglomerate of well-rounded pebbles, which has been assigned to the upper Eocene (EBERLE *et al.*, 1980). Additional studies indicate that the amber in these mines ranges from late Eocene (40 Ma) to late Oligocene (25 Ma) in age (LAMBERT *et al.*, 1985; BERGGREN *et al.*, 1985).

The seven fossils discussed here are in seven separate, worked pieces of amber designated as C-1, MO-1-1, MO-1-2, MO-1-3, MO-1-4, MO-1-5, and MO-1-6. Piece C-1 is roughly elliptical in shape, 2.7 cm × 1.6 cm × 0.7 cm, and weighs 1.9 g. Piece MO-1-1 is roughly elliptical, 3.7 cm × 1.8 cm × 1.1 cm, and weighs 4.3 g. Piece MO-1-2 is roughly hemispherical, 2 cm × 1.6 cm × 0.8 cm, and weighs 1.8 g. Piece MO-1-3 is elliptical, 3 cm × 1.3 cm × 1 cm, and weighs 2.6 g. Piece MO-1-4 is 2.3 cm × 1.6 cm × 1.0 cm, and weighs 2.1 g. Piece MO-1-5 is 1.0 cm × 1.4 cm × 0.5 cm, and weighs 0.6 g. Piece MO-1-6 is 2.4 cm × 2.3 cm × 0.8 cm, and weighs 2.9 g. All pieces were tested for authenticity using methods described earlier (POINAR, 1982). Specimens MO-1-1, MO-1-2, MO-1-3, MO-1-4, and MO-1-5 are in the Poinar collection of Dominican amber at the University of California, Berkeley.

Specimen C-1 is in the Costa collection in the Museum of Dominican amber in Puerto Plata, Dominican Republic. Specimen MO-1-6 is in the Brodzinsky collection of Dominican amber in Santo Domingo, Dominican Republic.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Subclass Pulmonata

Family STROBILOPSIDAE

Genus *Strobilops* Pilsbry, 1893

(?) Subgenus *Coelostrobilops* Pilsbry, 1927

Strobilops (?*Coelostrobilops*) sp.

(Figures 1, 2)

Specimen (MO-1-6) 1.8 mm in diameter, thin-shelled, depressed, with 4.25 whorls. Spire broadly conic; suture impressed. Periphery angulate; base convex. Embryonic whorls approximately 1.5, apparently unsculptured. Post-embryonic sculpture of fine, regularly spaced, threadlike, collabral ribs extending from suture to periphery, where they end abruptly. Aperture subcircular, oblique. Lip turned outward at about a right angle; inner lip scarcely impinging on umbilicus. Parietal callus thick, bearing two squarish lamellae; upper lamella much the larger. Palatal lip possibly with a basal plica. Umbilicus contained about 3.7 times in diameter.

Remarks—Soft tissues are contained in the shell, visible behind the apertural barriers.

The family Strobilopsidae has an extensive Recent and fossil distribution, reviewed by MANGANELLI *et al.*, (1989). The two parietal lamellae visible from the outside in apertural view, and the umbilicus more than one-fourth of the shell diameter, suggest assignment to the subgenus *Coelostrobilops* (type species: *Strobilops wenziana* Pilsbry, 1930). *Coelostrobilops* includes only two other known species, both Recent: *Strobilops salvini* (Tristram, 1863) from northern Guatemala, and *S. wenziana* from Grand Cayman Island. Two lamellae are also visible in the apertures of species of *Eostrobilops* Pilsbry, 1927, but in those species the shell is sculptured with irregular incremental rugae rather than distinct ribs.

This specimen represents the earliest unquestioned occurrence of Strobilopsidae in the Western Hemisphere. The late Cretaceous or early Paleocene *Strobilops mauryae* Ferreira & Dos Santos Coelho, 1971, from Brazil is based on incomplete shells, and its assignment to Strobilopsidae is questionable (MANGANELLI *et al.*, 1989). Two records of *Strobilops* from the Paleogene of the western interior of the United States (Hanley in TAYLOR, 1975; repeated by ROTH, 1986) prove to be erroneous. The specimens on which those records are based, from U.S. Geological Survey localities 20880 and 20881, an unnamed conglomeratic sequence of early Tertiary age along Little Granite Creek,

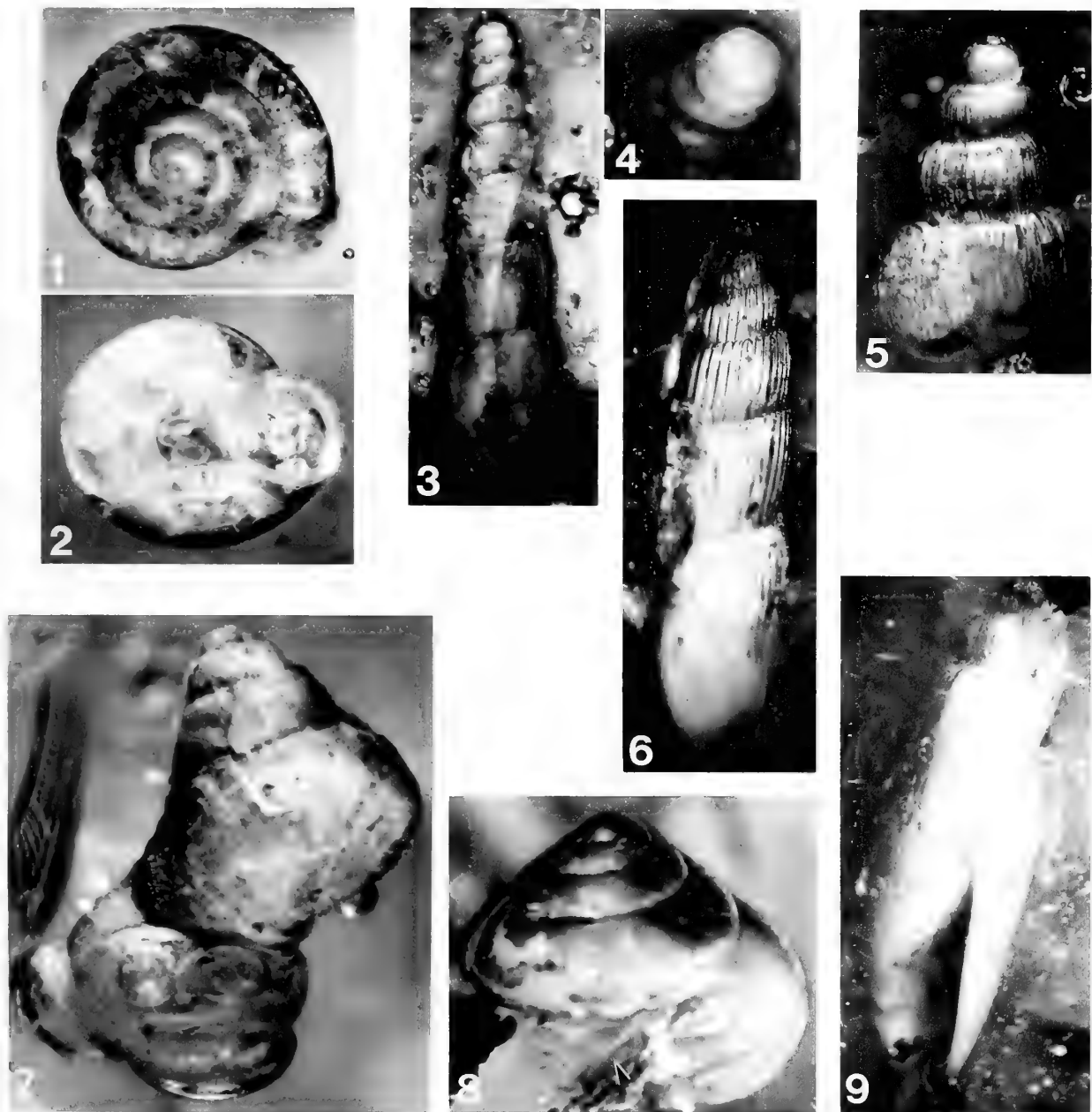
Hoback Basin, northwestern Wyoming, consist of seven specimens, probably representing three taxa. None shows the diagnostic internal lamellae of *Strobilops*. The two specimens from USGS 20881 are 2.28 mm and 2.77 mm in diameter, with sinuous transverse major ribs approximately 0.19 mm apart on the body whorl with 3–5 minor ribs in the interspaces. Compound ribbing of this type is not known in the Strobilopsidae. One specimen from USGS 20880 is a flattened, discoidal shell 3.15 mm in diameter, with sinuous, widely separated, threadlike transverse ribs approximately 0.16 mm apart, and parallel spiral striation that is absent from the last half whorl and may actually be a subsurface feature partly exposed by erosion. The four other specimens from USGS 20880 are depressed-helicoid shells with closely spaced ribs about 0.02 mm wide and interspaces of equal width. The ribbing is as strong on the base as on the spire. One shows faint spiral striation in the interspaces. Another has a 0.3-mm-long spiral lamella inside the shoulder of the body whorl, about 0.1 mm back from the aperture, but no evidence of basal or parietal lamellae. The barrier is more suggestive of the lamellae in certain Helicodiscidae, or perhaps Megomphicidae.

The next earliest records of *Strobilops* in the Americas are of Blancan (Pliocene, <5 Ma) age from Florida and Kansas (TAYLOR, 1966).

The presence of a species of *Strobilops* in the Paleogene of Mesoamerica requires modification of the historical biogeographic hypothesis advanced for the Strobilopsidae by MANGANELLI *et al.*, (1989). Rejecting PILSBRY's (1948) earlier concept of an Asian origin for the family, those authors suggested that the Strobilopsidae originated in the late Cretaceous or early Tertiary in an area of Laurasia corresponding to present-day Europe, before the opening of the North Atlantic Ocean had isolated North America from Europe. They attributed the presence of Strobilopsidae in Central America to later dispersal (presumably, from North America). Similarly, SOLEM (1979a, b, 1981) regarded the Strobilopsidae as a group that had "moved" from its region of origin to a present limit of distribution several thousand kilometers distant.

However, based on the present specimen, the earliest occurrence of the family in the Western Hemisphere is Mesoamerican. The earliest generally accepted Strobilopsidae, from the Lutetian and Bartonian (middle Eocene, >40 Ma) of western Europe are all assigned to the extinct genus or subgenus *Paleostrobilops* Wenz, 1923 (type species: *Helix menardi* Brongniart, 1810); they have more complex internal barrier systems than any extant genera or subgenera. The earliest fossil strobilopsids assignable to extant genera are post-Bartonian: *Strobilops* (*Strobilops*) *haedonensis* (Edwards, 1852) and *S. (S.) pseudolabyrinthica* (Sandberger, 1873) from the Tongrian, late Eocene to early Oligocene, 38–35 Ma (BERGGREN *et al.*, 1985).

Depending on the age of the present specimen, then, strobilopsid land snails assignable to modern taxa may have been present in the American tropics at least as early as in western Europe. They probably formed part of an



Explanation of Figures 1-9

Figures 1, 2. *Strobilops* (?*Coelostrobilops*) sp. (MO-1-6). Top and basal views. Diameter 1.8 mm.

Figures 3, 4. *Subulina* sp. (MO-1-2). Lateral and apical views. Height 11.5 mm.

Figure 5. *Spiraxis* sp. (MO-1-3). Lateral view. Height 3.1 mm.

Figure 6. *Varicella* sp. (MO-1-1). Lateral view. Height 10 mm.

Figure 7. Prosobranch land snail, indeterminate (MO-1-5). Oblique lateral view showing soft tissues and associated gas bubbles. Height of shell 3.5 mm.

Figure 8. Helicinid, genus and species indeterminate (C-1). Oblique apertural view. Diameter 3.0 mm. Operculum at arrow.

Figure 9. ?*Ferussaciid*, genus and species indeterminate (MO-1-4). Lateral view. Height 7.6 mm.

early Tertiary land mollusk fauna that was arrayed across the southern part of North America, roughly parallel to the western limb of the Tethyan seaway (ROTH, 1986, 1988). Rather than having "moved" (as per SOLEM, 1979a), they may have undergone mainly a southward restriction of their northern range limit, perhaps accompanying cooling climates through the Tertiary period.

This model further suggests that the cold-tolerance and northern distribution of such forms as *Strobilops labyrinthica* (Say, 1817) and *S. affinis* Pilsbry, 1893, of the eastern United States is a secondarily derived attribute. This suggestion could be falsified by the finding of strobilopsids of this clade in rocks of late Eocene or older age in eastern North America (where, unfortunately, terrestrial deposits of the requisite age are rare). A phylogenetic hypothesis for the members of the Strobilopsidae will have to be devised before the temporal relationships between tropical and extratropical, American and European groups can be further resolved.

Family SUBULINIDAE

Genus *Subulina* Beck, 1837

Subulina sp.

(Figures 3, 4)

Specimen (MO-1-2) 11.5 mm long, 2.3 mm in greatest diameter; opaque, whitish. Lanceolate, slender, straight-sided, with 8+ evenly rounded, rather convex whorls, tapering to a blunt apex. Suture appressed, crenulated by a series of short, fine, subsutural folds. Aperture about 25% of total height. Prominent collabral lines, representing growth rests, present on penult and body whorl.

Remarks—The specimen is remarkably similar to the Recent species *Subulina octona* (Bruguière, 1792). It differs in the body whorl being slightly higher in proportion to total shell height. The buttonlike nuclear tip, nearly immersed in a globose first embryonic whorl, and the fine short folds that crenulate the suture are characteristic of the genus. Soft tissue around the aperture obscures details of the columella.

The present range of *Subulina* includes the American tropics. There appears to be no prior record of the genus as fossils. Recent species of *Subulina* live in ground litter in moist places.

Family SPIRAXIDAE

Genus *Spiraxis* C. B. Adams, 1850

Spiraxis sp.

(Figure 5)

Specimen (MO-1-3) 3.1 mm long, 1.6 mm in greatest diameter, apparently rather solid, with 4.5 whorls (only spire present, base truncated by edge of matrix). Steeply conic, with deeply impressed to channeled suture; whorls narrowly shouldered. Embryonic whorls approximately 1.5, globose, apparently unsculptured. Postembryonic

sculpture of narrow, rather crowded, axial ribs, weak at first but after 0.5 whorl becoming continuous across whorls, crenulating suture.

Remarks—Apertural characters are not preserved. In its smooth protoconch, deeply impressed suture, and rather straight-sided whorls, this specimen resembles some Recent species such as *Spiraxis subrectaxis* Pilsbry, 1930, from Grand Cayman Island. It is, however, more broadly conic than is typical for modern species.

The present range of *Spiraxis* includes Cuba, Jamaica, and other islands of the West Indies. There is no prior record of fossils of the genus (ZILCH, 1959–1960). Recent species of *Spiraxis* are typically found among plant debris on the ground (e.g., PILSBRY, 1930).

(?) Family FERUSSACIIDAE

?Ferussaciid, genus and species indeterminate

(Figure 9)

Specimen (MO-1-4) 7.6 mm in height, 2.2 mm in greatest diameter, opaque, cream-white, solid, with about 5 whorls. Elongate, ovate-cylindrical, with strongly impressed suture and narrowly, almost tabulately shouldered whorls. Embryonic whorls apparently 2, carinate at shoulder, with close-set, sharp, axial ribbing. Postembryonic whorls smooth, with regularly spaced, incised, axial striations. Aperture about 60% of total height, narrow, pear-shaped, acute posteriorly, rounded anteriorly; outer lip apparently somewhat thickened within; basal lip produced; parietal wall with smooth callus; columella deeply arched, not truncated.

Remarks—This specimen is referred questionably to Ferussaciidae on the basis of size and overall shape, relative height of body whorl, and shape of aperture and columella. However, the axially sculptured, shouldered embryonic whorls and the incised sculpture of the teleoconch are unlike anything heretofore reported in that family. The compressed ribbing resembles that of some modern species of *Varicella* Pfeiffer, 1856 (Oleacinidae). A keeled, ribbed protoconch occurs in some groups of Bulimulidae (e.g., subgenus *Plicolumna* Cooper, 1895, of *Rabdotus* Albers, 1850), but the present shell is not otherwise bulimuloid. The specimen may belong to an undescribed, extinct group, perhaps in Achatinoidea or Oleacinoidea.

The Ferussaciidae are a pantropical group with a few genera in Mesoamerica (ZILCH, 1959–1960). Eocene through Miocene fossils are known from Europe. Recent species are ground-dwelling; some are fossorial.

Family OLEACINIDAE

Genus *Varicella* Pfeiffer, 1856

Varicella sp.

(Figure 6)

Specimen (MO-1-1) 10 mm in height, 3.1 mm in greatest diameter, translucent but solid, fusiform, without about 7

whorls. Spire narrowly conic, convex-sided; suture deeply impressed, crenulated by ribs; whorls narrowly shouldered. Embryonic whorls about 2, projecting, smooth, globose. Postembryonic sculpture of strong, smooth, regularly spaced, shallowly sinuous, collabral ribs. Body whorl about 35% of height of shell, compressed, produced anteriorly; ribs becoming weaker on body whorl. Aperture narrow, pear-shaped; outer lip convex in profile, thickened outside and within; basal lip smoothly rounded; columella arched.

Remarks—The Recent range of *Varicella* includes Jamaica, central and eastern Cuba, Hispaniola, and Puerto Rico. There is no prior record of fossils of the genus (ZILCH, 1959–1960). Most Recent species of *Varicella* are ground-dwelling (BAKER, 1941, 1962), but the Jamaican *Varicella* (*Costavarix*) *adamsiana* is reported to be a “fair climber, at least occasionally” (BAKER, 1935).

Subclass Prosobranchia

Family HELICINIDAE

Helicinid, genus and species indeterminate

(Figure 8)

Specimen (C-1) 2.5 mm in height, 3.0 mm in diameter, thin-shelled, translucent, light brown, trochoid, with slightly more than 4 whorls. Spire broadly conic; suture weakly impressed; whorls flattened. Nuclear tip prominent, tumid. Periphery subangulate, grading to rounded on last whorl; base flattened. Surface practically unsculptured, except for faint incremental lines; stronger collabral lines, representing growth rests, present 0.5 and 0.7 whorls back from edge of lip. Aperture gibbous; lip unthickened above; basal lip slightly calloused, left edge produced, with shallow sinus at junction with columellar lip. Base imperforate, apparently with small callus pad in umbilical region.

Remarks—Soft tissue extends outside the aperture, and a solid, discoidal structure, here interpreted as an operculum, lies near the base of the body whorl, in front of the aperture (Figure 8, arrow). If the living animal were partly extended, one would expect to find the operculum in a similar position. With its relatively unthickened lip, the specimen is probably immature. It cannot be assigned to a specific genus, but the available characters are consistent with several genera of the subfamily Helicininae, such as *Helicina* Lamarck, 1799, and *Olygyra* Say, 1818.

The present range of the subfamily Helicininae includes the American and east Asian tropics and Pacific Islands. Considerable diversity occurs in Central America and the Greater Antilles. Helicinidae have an extensive and complex fossil record in North America, extending back to late Cretaceous time (ROTH, 1986; ROTH & PEARCE, 1988; PIERCE & RASMUSSEN, 1989). The generic allocation of many of the described fossils is uncertain (as PIERCE & RASMUSSEN, 1989, noted) and much further study is necessary before a phylogenetic hypothesis and biogeographic history can be postulated.

Some Recent species are known to ascend trees (PILSBRY, 1948; Roth, personal observations).

Family Indeterminate

Prosobranch land snail, genus and species indeterminate

(Figure 7)

Specimen (MO-1-5) approximately 3.4 mm in height, 2.8 mm in diameter, thin-shelled, brown, conical, with about 4 whorls. Apex blunt (sculpture eroded); suture moderately impressed; whorls narrowly shouldered. Postembryonic sculpture of narrow, close-set, axial ribs, apparently slightly beaded. Base inflated, possibly umbilicate. Lip apparently simple; shape of aperture obscured by soft tissue.

Remarks—The specimen is cracked from compression. Soft tissue, distorted by a gas bubble within, extends from the aperture. A flat structure that we interpret as an operculum is present a short distance outside the aperture.

The presence of an operculum indicates that the specimen is a prosobranch. The conical shape and beaded axial sculpture suggest an immature member of the family Annulariidae, but the absence of details of the adult aperture or of the operculum make it impossible to rule out high-spired Poteriidae such as *Megalomastoma* Swainson, 1840, or other taxa (cf. WENZ, 1938–1944). Both the Poteriidae and Annulariidae are at present restricted to the American tropics and are diverse in the Greater Antilles. Neither has a fossil record.

DISCUSSION

The land snail taxa indicate a tropical or paratropical climate. All the identified genera include Hispaniola or other Antillean islands in their Recent ranges. The occurrence of a frog of the tropical American genus *Leptodactylus* in amber from the El Mamey Formation (POINAR & CANNATELLA, 1987) is consistent with this climatic interpretation.

Of the snails described here, the *Varicella* and helicinid species might plausibly be considered arboreal snails. Species of Subulinidae are mainly predaceous, ground-dwelling forms, and not normally found in trees. Strobilopsidae and Spiraxidae are predominantly found among plant litter on the ground. According to LARSSON (1978), the snails reported from Baltic amber are also forest-floor dwellers found among rotting plant remains or in moss at the bases of trees. Most likely, these snails crawled in under the loose bark of logs or stumps seeking shelter, and there became entangled in resin.

The association of snails and resin is noteworthy in itself. Modern forests dominated by highly resinous (e.g., coniferous) trees tend to have low land snail diversity (SOLEM, 1984).

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Late Quaternary *Chaenaxis tuba* (Pupillidae) from the Sonoran Desert, South-Central Arizona

by

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Abstract. Shells of *Chaenaxis tuba* Pilsbry & Ferriss, 1906 (Pupillidae) were recovered from five radiocarbon-dated packrat (*Neotoma*) middens from the Waterman Mountains, northeastern Sonoran Desert, Pima County, Arizona. Associated plant macrofossils indicate that *C. tuba* has been present in rocky limestone habitats for 11,470 yr as the local vegetation shifted from a pinyon-juniper woodland in the late Wisconsin glacial to a postglacial juniper woodland/chaparral in the early Holocene (9920 yr B.P.) to a mesic Sonoran desertscrub in the middle Holocene (8910 to 4845 yr B.P.) to a modern desertscrub in the late Holocene (1320 yr B.P.). *Chaenaxis tuba* persisted in the community in spite of the climatic and vegetational changes within the local habitat.

INTRODUCTION

Fossil packrat (*Neotoma* spp.) middens have proven to be a rich source of fossils from the deserts of the southwestern United States and northern Mexico (see references in BETANCOURT *et al.*, 1990). In the Sonoran Desert of Arizona, detailed reconstructions of vegetation and climate for the last 40,000 yr have been developed using abundant plant macrofossils from middens. Mesic ice-age pinyon-juniper-oak woodlands were replaced by more xeric juniper woodland/chaparral in the early Holocene (11,000-9000 yr B.P. = radiocarbon years before 1950 A.D.). Although Sonoran desertscrub developed after 9000 yr B.P., relatively modern communities were not present until about 4000 yrs ago (VAN DEVENDER, 1990). Various small vertebrates have been identified from Sonoran Desert middens from Arizona and California (VAN DEVENDER & MEAD, 1978; MEAD *et al.*, 1983; VAN DEVENDER *et al.*, in press a, b). Midden arthropods have been identified from five areas in southwestern Arizona and northwestern Sonora (HALL

et al., 1988, 1989, 1990). In this paper, we report land snail shells from packrat middens from the Waterman Mountains of Arizona.

MATERIALS AND METHODS

Packrat middens are hard, dark organic deposits produced by various species of *Neotoma* (Rodentia, Cricetidae). In open areas, packrats build protective houses out of various plants, rocks, and animal remains collected within a forage distance of 30-50 m (FINLEY, 1958). Portions of dens constructed in dry rockshelters and crevices can be cemented with urine and preserved for tens of millennia (VAN DEVENDER *et al.*, 1987). Chronological series of radiocarbon-dated assemblages (MEAD *et al.*, 1978; VAN DEVENDER *et al.*, 1985; WEBB & BETANCOURT, 1990) can be used to reconstruct the local vegetation and fauna of rocky slopes through time.

Snail shells were recovered from six packrat middens from the Waterman Mountains (WAM), Pima County,

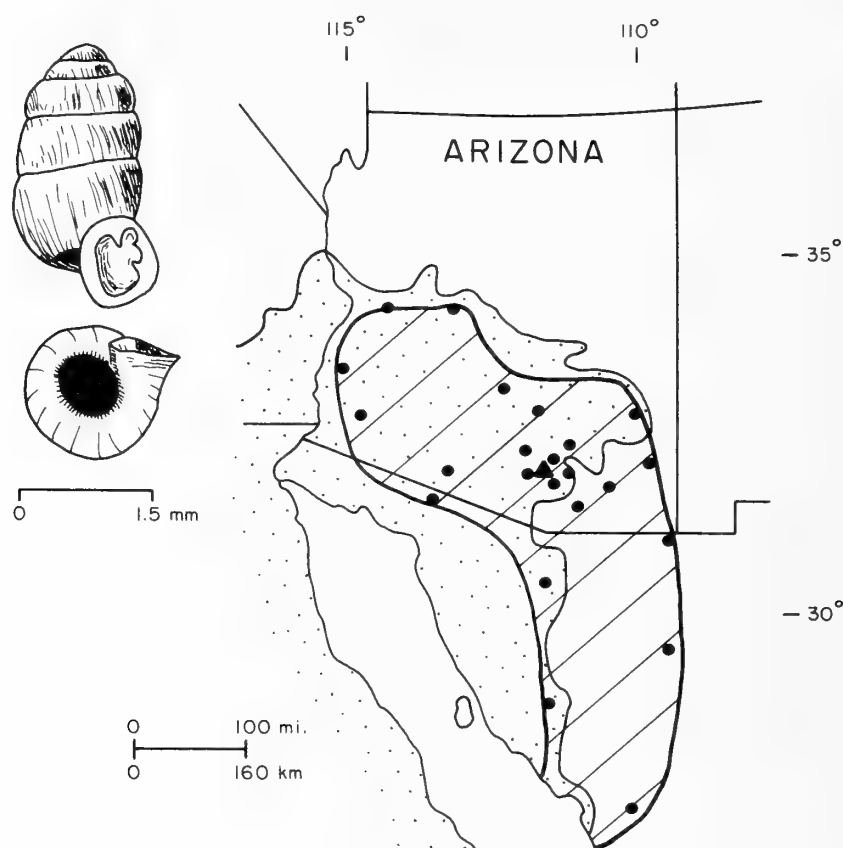


Figure 1

Distribution of *Chaenaxis tuba* in Arizona and Sonora, Mexico. Stippled region represents the outline of the Sonoran Desert (TURNER & BROWN, 1982). Hachured area represents the overall range of *C. tuba*; large dots indicate the primary localities from BEQUAERT & MILLER (1973) and the Waterman Mountains. Solid triangle is the midden location northwest of Tucson. Line drawings of *Chaenaxis* after PILSBURY & FERRISS (1906).

Arizona (32°20'30"N, 111°27'W). The samples were disaggregated in water, screened through a 20-mesh soil sieve, and sorted by hand. Radiocarbon dates on *Neotoma* sp. fecal pellets and *Stipa speciosa* (desert needlegrass) florets ranged in age from the latest Wisconsin glacial (11,470 yr B.P.) to the postglacial late Holocene (1320 yr B.P.; Table 1). Although *Chaenaxis tuba* shells were not directly radiocarbon dated, the plant assemblages do not appear to be drastically mixed, an indication of only slight temporal contamination. Pollen and plant macrofossils from the middens were studied by ANDERSON & VAN DEVENDER (1991).

The Waterman Mountains are in the Arizona Upland subdivision in the northeastern Sonoran Desert (SHREVE, 1964; TURNER & BROWN, 1982). The local vegetation is a rich, structurally diverse desertscrub dominated by *Cercidium microphyllum* (foothills paloverde), *Encelia farinosa* (brittlebrush), *Olneya tesota* (ironwood), *Fouquieria splendens* (ocotillo), *Carnegiea gigantea* (saguaro), and *Parthenium incanum* (mariola). The midden crevices are in both

the shady north-facing (WAM 1) and exposed south-facing (WAM 9 and 10) cliffs at 790 m elevation on a steep east-west oriented limestone ridge.

Modern litter samples from the cliff bases were screened and sorted for mollusk shells. *Chaenaxis tuba* was the only species recovered in litter from both slopes. Fossil and modern snails were identified through comparison with modern specimens at the Northern Arizona University, Laboratory of Quaternary Paleontology collection. Specimens were deposited into this collection.

RESULTS AND DISCUSSION

All of the midden shells are the monotypic *Chaenaxis tuba*, a tiny snail of the family Pupillidae described by PILSBURY & FERRISS (1906) as a subgenus of *Bifidaria* from drift along the San Pedro River, opposite the Dragoon Mountains in Cochise County, Arizona. The shell of *C. tuba* has a hollow, broadly open umbilicus, which is diagnostic for the genus and nearly unique in the Pupillidae (BEQUAERT

Table 1

Radiocarbon ages (years before 1950 = yr B.P.) for packrat middens containing *Chaenaxis tuba* shells from the Waterman Mountains, Pima County, Arizona. Dominant plants in the midden assemblages in order of decreasing relative abundances: 5 = abundant, 4 = very common, 3 = common, 2 = uncommon.

Sample	Lab no. ^a	Radiocarbon age (yr B.P.)	Material dated	Paleovegetation	Dominant plants
9A2	A-4777	11,470 ± 170	<i>Neotoma</i> sp. dung	Pinyon-juniper woodland	<i>Acacia greggii</i> (5) <i>Juniperus</i> sp. (5) <i>Brickellia coulteri</i> (3) <i>Lycium</i> sp. (3) <i>Vauquelinia californica</i> (3) <i>Pinus monophylla</i> (2)
9B	A-4776	9920 ± 130	<i>Neotoma</i> sp. dung	Juniper woodland/chaparral	<i>Juniperus</i> sp. (5) <i>Acacia greggii</i> (4) <i>Brickellia coulteri</i> (3) <i>Rhus</i> cf. <i>aromatica</i> (3) <i>Berberis</i> sp. (2)
9C	A-4779	8910 ± 110	<i>Neotoma</i> sp. dung	Mesic Sonoran desertscrub	<i>Acacia greggii</i> (5) <i>Encelia farinosa</i> (5) <i>Lycium</i> sp. (4) <i>Rhus</i> cf. <i>aromatica</i> (4) <i>Crossosoma bigelovii</i> (3) <i>Sphaeralcea</i> sp. (3)
10	AA-3353	8360 ± 135	<i>Stipa speciosa</i> florets	Mesic Sonoran desertscrub	<i>Acacia greggii</i> (5) <i>Ferocactus cylindraceus</i> (5) <i>Encelia farinosa</i> (4)
	A-4780	8260 ± 130	<i>Neotoma</i> sp. dung		<i>Lycium</i> sp. (3)
	AA-3353, A-4780 ^b	8310 ± 95			<i>Rhus</i> cf. <i>aromatica</i> (3)
9D	A-4781	5540 ± 70	<i>Neotoma</i> sp. dung	Mesic Sonoran desertscrub	<i>Carnegiea gigantea</i> (5) <i>Cercidium floridum</i> (4) <i>Encelia farinosa</i> (4)
	AA-3354	4845 ± 80	<i>Stipa speciosa</i> florets		<i>Acacia greggii</i> (3)
	A-4781, AA-3354 ^b	5190 ± 55			<i>Bursera</i> cf. <i>microphylla</i> (3) <i>Ferocactus cylindraceus</i> (3) <i>Hyptis emoryi</i> (3) <i>Opuntia versicolor</i> (3) <i>Prosopis velutina</i> (3)
1E	A-4558	1320 ± 45	<i>Neotoma</i> sp. dung	Modern desertscrub	<i>Lycium</i> cf. <i>berlandieri</i> (5) <i>Carnegiea gigantea</i> (4) <i>Cercidium microphyllum</i> (4) <i>Opuntia phaeacantha</i> (4) <i>Ferocactus cylindraceus</i> (3) <i>Jatropha cardiophylla</i> (3) <i>Olneya tesota</i> (3)

^a Radiocarbon codes: A, conventional radiocarbon method; AA, accelerator mass spectrometer method.

^b Dates averaged by the method of LONG & RIPPETEAU (1974).

& MILLER, 1973; Figure 1 herein). The cylindrical or slightly tapering shell varies greatly in size and shape within a population. BEQUAERT & MILLER (1973) placed this species in the subfamily Pupillinae on the basis of its internal anatomy rather than in the Gastrocoptinae as implied by PILSBRY (1948). They hypothesized that *Chaenaxis* evolved in Arizona within the Southwestern Molluscan Province. The Waterman Mountains midden specimens are the first fossil records for the genus.

Today, *Chaenaxis tuba* is known from 460 to 1470 m elevation from southern Arizona and eastern Sonora. In the Sonoran Desert in Arizona, it has been found living

under rocks and leafy plants in arid foothills and desert mountain ranges in portions of the Lower Colorado River Valley and Arizona Upland subdivisions receiving 100–300 mm/yr precipitation. Our modern Waterman Mountains collections are a new locality. In Sonora, Mexico, it has been collected at 275 m in the Plains of Sonora subdivision near Hermosillo (PILSBRY, 1953; BRANSON *et al.*, 1964). In central and southeastern Arizona, *C. tuba* can be found in higher, wetter (>400 mm/yr) habitats ranging from Interior Chaparral (PASE & BROWN, 1982) below the Mogollon Rim to a complex mixture of Chihuahuan and Sonoran desertscrub, desert-grassland, and Madrean

oak woodland in southeastern Arizona. In desert-grassland on limestone slopes at 1465 m in the Dos Cabezas Mountains, Cochise County, southeastern Arizona, we found *C. tuba* under *Dasyllirion wheeleri* (sotol) and *Nolina microcarpa* (beargrass). Prominent shrubs and succulents included *Acacia greggii* (catclaw acacia), *A. neovernicosa* (Chihuahuan whitethorn), *Cercocarpus montanus* (mountain mahogany), *Fouquieria splendens*, *Mortonia sempervivens* (sandpaper bush), *Prosopis glandulosa* (honey mesquite), *Quercus turbinella* (shrub live oak), *Rhus aromatica* (skunk bush), and *Agave palmeri* (century plant). *Chaenaxis tuba* has also been found in eastern Sonora along the elevational gradient from lowland subtropical Sinaloan thornscrub to montane temperate woodlands and forests in the Sierra Madre Occidental.

Snail shells have rarely been found in packrat middens. Plant macrofossils associated with the shells of *Chaenaxis tuba* provide a history of the local vegetation in its rocky, limestone habitat for the Holocene. Six late Wisconsin glacial middens (22,450 to 11,470 yr B.P.) in the Waterman Mountains record a pinyon-juniper woodland dominated by *Juniperus osteosperma* (Utah juniper) and *Pinus monophylla* (singleleaf pinyon) in association with such chaparral plants as *Quercus turbinella*, *Rhus* cf. *aromatica*, and *Vauquelinia californica* (Arizona rosewood). *Chaenaxis tuba* was not found in five older late Wisconsin midden samples (implying that older *Chaenaxis* shells were not being mixed into younger, <11,500 yr B.P., midden assemblages).

The appearance of *Chaenaxis tuba* in the area correlates well with the arrival of *Prosopis velutina* (velvet mesquite), a desert-grassland dominant directly dated on seeds at $11,740 \pm 110$ yr B.P. (AA-3577). The local vegetation shifted to a juniper woodland/chaparral dominated by *Juniperus* cf. *erythrocarpa* (redberry juniper) in the early Holocene (9920 yr B.P.), to a mesic Sonoran desertscrub in the middle Holocene (8910 to 4845 yr B.P.) and to a relatively modern desertscrub in the late Holocene (1320 yr B.P.). The modern vegetation reflects a more xeric climate than any of the midden assemblages.

Our conclusions rest on the assumption that the *Chaenaxis* shells are contemporaneous with each of the midden assemblages. This assumption is justified for two reasons: (1) five of the oldest middens, from the same series, do not contain *Chaenaxis* shells, and (2) multiple radiocarbon dates from two middens do not indicate drastic temporal mixing. The late Wisconsin-to-modern vegetation development in the Waterman Mountains includes most of the vegetation types presently known for *C. tuba*. The continued presence of this tiny pupillid in the study area is testimony to its successful adaptation to a xeric, rocky habitat rather than to a particular vegetation type or climatic regime.

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Generic Identity and Relationships of the Northeastern Pacific Buccinid Gastropod *Searlesia dira* (Reeve, 1846)

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Abstract. The buccinid gastropod genus *Searlesia* Harmer, 1914, contains about a dozen nominal species from the Oligocene to the Pliocene of Europe, with type species *Trophon costifera* S. V. Wood, 1848. Oligocene to Recent species assigned to *Searlesia* from the North Pacific differ consistently from the European species by having an internally lirate aperture and a simple, rather than thickened or reflected, adult lip. The Pacific species are here assigned to the new genus *Lirabuccinum*, with type species *Buccinum dirum* Reeve, 1846, from the northeastern Pacific. Suggestions that *Lirabuccinum* invaded the Atlantic during the Pliocene, when it gave rise to European species of *Searlesia*, are rejected in favor of the hypothesis that the two genera evolved separately in the Atlantic and Pacific oceans respectively and remained confined to the oceans in which they originated. The name *Searlesia dentifera* is here proposed to replace *Searlesia ravni* Schnetler in Schnetler & Beyer, 1990, non Harmer, 1914.

INTRODUCTION

The genus *Searlesia* Harmer, 1914, was erected to encompass *Trophon costiferum* Wood, 1848, and about a dozen other species from the Pliocene of the North Sea basin and Iceland (HARMER, 1914-1923). All twentieth-century authors have considered *Searlesia* to belong to the Buccinidae. In his initial treatment of the genus in 1914, Harmer alluded to a letter from W. H. Dall in which Dall expressed the view that *Buccinum dirum* Reeve, 1846, a common Recent northeastern Pacific species, should be included in *Searlesia* along with the European Pliocene fossils. DALL (1916, 1918) reaffirmed this assignment of *B. dirum* to *Searlesia* in his review of North Pacific buccinids, and in 1918 he added a second Recent species, *S. constricta* Dall, 1918, from Korea. All subsequent workers have accepted the assignment of *B. dirum* to *Searlesia*. Several additional species from western North America and eastern Asia were subsequently described, with the result that the stratigraphical range of the Pacific members of *Searlesia* came to be regarded as Oligocene to Recent.

Dall probably had no specimens of *Searlesia costifera* with which to compare *Buccinum dirum*, and therefore seems to have relied wholly on the illustrations and descriptions supplied to him by Harmer. This may explain why Dall overlooked, or failed to appreciate, the differ-

ences in shell form between the two species, which are superficially very similar.

In order to assess the taxonomic position of the European and Pacific species assigned to *Searlesia*, I examined all type specimens of species referred to *Searlesia* and *Calicantharus* at the U.S. National Museum of Natural History (USNM), Washington, and at the Museum of Paleontology, University of California, Berkeley (UCB). In addition, I examined species of *Pirgos* and related European buccinids at the National Museum voor Natuurlijke Historie (NMNH), Leiden, and species of *Searlesia* and *Calicantharus* at the California Academy of Sciences (CAS), San Francisco. Assignments of Oligocene European species and of fossil Asian species were based on descriptions in the literature. Although the descriptions are adequate for generic assignments, I have not attempted a full-scale review of all described species. Not only were type specimens not available for many of them, but several taxa are based on so few specimens that it would have been impossible to decide on the basis of the available material whether individuals belong to one or a few variable species or to many closely related but phenotypically rather homogeneous species.

In this paper, I shall try to show that the European and Pacific species now generally included in *Searlesia* belong to two lineages with long separate histories, one in Europe

(*Searlesia*), the other in the temperate North Pacific. I propose *Lirabuccinum* [type species: *Buccinum dirum* Reeve, 1846] as a new genus to encompass the latter group. The biogeographical implications of this new interpretation are briefly considered at the end of the paper.

SYSTEMATICS

Genus *Searlesia* Harmer, 1914

Type species: *Trophon costiferum* Wood, 1848.

Description: Shell fusiform; protoconch eroded and therefore unknown; teleoconch whorls somewhat tabulate; axial sculpture of narrowly rounded straight orthocline folds that on the spire whorls extend suture to suture and on the body whorl extend only part of the way toward the base; axial folds variable in number, prominence, and ontogenetic extent; spiral sculpture of numerous thin cords and secondary threads crossing the axial folds; adult outer lip slightly thickened or reflected, smooth within; inner lip weakly concave, smooth; siphonal canal straight, not deflected to the left, not curved upward at end, not distinctly set off from rest of shell; no posterior notch; operculum and animal unknown.

Composition and comparisons: HARMER (1914–1923) assigned 10 species to the genus *Searlesia*, all from the Pliocene of the North Sea basin and from the Pliocene of Iceland (see also GLADENKOV *et al.*, 1980). These species, together with their places and times of occurrence, are listed in Table 1. I have not critically reviewed these species, but I am highly skeptical that they are all distinct. Harmer noted intermediates between some of them, and many were described on the basis of one or two specimens. Many Recent buccinids show great intrapopulational variation in spire height and in the expression of axial sculpture, just the characteristics used by Harmer in distinguishing among his species.

JANSSEN (1979) added *Searlesia mitgauti* (von Koenen, 1867), from the late Oligocene (Chatian) of Germany, to the genus. This species has the outer lip smooth on its inner surface, and bears sculpture similar to that of *S. costifera*. It apparently continued into the early Miocene of Belgium, where it was represented by *Euthria antwerpensis* Glibert, 1952, a probable synonym of *S. mitgauti* according to JANSSEN (1979).

Two additional Oligocene species have subsequently been added by SCHNETLER & BEYER (1990). *Searlesia konincki* (Nyst, 1845) from the Rupelian of Belgium and Germany and *S. ravni* Schnetler in Schnetler & Beyer, 1990, from the late Oligocene (Chatian) of Denmark, share with *S. mitgauti* the presence of a small parietal tooth. This feature is not seen in *S. costifera*. It may be that these three Oligocene species should be referred to a distinct genus or subgenus (see also SCHNETLER & BEYER, 1990). Unfortunately, Schnetler's *S. ravni* is a primary homonym of *S. ravni* Harmer, 1914, a Pliocene species. In view of

Table 1

List of the nominal species of *Searlesia*.

<i>S. bjornsoni</i> Mörch & Poulsen in Harmer, 1914: late Pliocene (Waltonian to Butleyan Red Crag of England, <i>Serripes</i> zone of Tjörnes section, Iceland).
<i>S. costifera</i> (Wood, 1848) (type): early Pliocene (Coralline Crag of England; <i>Mactra</i> zone of Tjörnes section, Iceland); late Pliocene (Waltonian to Butleyan Red Crag of England; Isle of Man).
<i>S. elegans</i> Harmer, 1914: late Pliocene (Waltonian Red Crag of England).
<i>S. forbesi</i> (Strickland, 1846): late Pliocene (Waltonian Red Crag of England; Isle of Man).
<i>S. harrisoni</i> A. Bell in Harmer, 1914; late Pliocene (Isle of Man).
<i>S. konincki</i> (Nyst, 1845): middle Oligocene (Rupelian, western Europe).
<i>S. lundgreni</i> Mörch & Poulsen in Harmer, 1914: early Pliocene (<i>Mactra</i> zone of Tjörnes section, Iceland); late Pliocene (<i>Serripes</i> zone, Tjörnes section, Iceland).
<i>S. mitgauti</i> (von Koenen, 1867): late Oligocene (Chatian, Germany); early Miocene, Belgium.
<i>S. nordmanni</i> Harmer, 1914: late Pliocene (Waltonian Red Crag of England; Isle of Man).
<i>S. oyeni</i> Harmer, 1914: late Pliocene (Isle of Man).
<i>S. proxima</i> Harmer, 1914: late Pliocene (Waltonian Red Crag of England).
<i>S. ravni</i> Harmer, 1914: early Pliocene (Coralline Crag of England); late Pliocene (Waltonian Red Crag of England).
<i>S. dentifera</i> Vermeij, 1991, new name: late Oligocene (Chatian, Denmark).

the tooth on the parietal wall of the Oligocene species, I here propose the replacement name *S. dentifera*, new name, for the Danish species.

The species *Searlesia forbesi* (Strickland, 1846) was said by HARMER (1914–1923) to differ from *S. costifera* and other species of *Searlesia* by the denticulation of the outer lip of the adult. It is unclear from his description and illustrations if this denticulation is in the form of small teeth, which would be discontinuous in the spiral direction, or if they represent spirally continuous lirae. For the time being I regard *S. forbesi* as a *bona fide* *Searlesia*.

HARMER (1914–1923) doubtfully included *Fusus alveolatus* Sowerby, 1829, and *Trophon consocialis* Wood, 1848, both ranging from the late Miocene to the late Pliocene of the North Sea basin, in his genus *Searlesia*. Previously, however, DE GREGORIO (1885) had erected the genus *Pirgos* [type species: *F. alveolatus*] to encompass these species, and several authors have retained this assignment (VAN REGTEREN ALTENA *et al.*, 1957; GLIBERT, 1963). Harmer was evidently unaware of de Gregorio's taxon *Pirgos*, for otherwise he might have chosen it to include *S. costifera* and related British forms. Species of *Pirgos* differ from *S. costifera* by having more numerous axial ribs and sharper, more distantly spaced spiral ribs, which cross to form a beaded sculpture.

Because of similarities in the ontogeny of spiral and axial sculpture, TEMBROCK (1968) regarded *Pirgos* as a

subjective junior synonym of *Scalaspira* Conrad, 1862 [type species: *S. strumosa* (Conrad, 1831, early Pliocene Yorktown Formation, Virginia)]. She further suggested that the species previously placed in *Pirgos* belong to a lineage beginning with *S. elegantula* (Philippi, 1843) from the late Oligocene of Germany. The latter species, together with many other species from the Oligocene and Miocene of western Europe, had previously been assigned to *Aquilofusus* Kautsky, 1925 [type species: *A. puggaardi* (Beyrich, 1856)], which TEMBROCK (1968) also synonymized under *Scalaspira*.

In her greatly expanded concept of *Scalaspira*, TEMBROCK (1968) brought together gastropods ranging in age from Eocene to Recent in the Atlantic and from Oligocene to Recent in the North Pacific. In addition to *Pirgos*, *Aquilofusus*, and the Miocene and Pliocene western Atlantic species of *Scalaspira*, she included in *Scalaspira* the genera *Mohnia* Friele in Kobelt, 1878 [type species: *M. mohni* (Friele, 1877)] from the Recent North Atlantic and the Pliocene to Recent of the North Pacific; *Troschelia* Mörch, 1877 [type species: *T. bernicensis* (King, 1846)] from the late Pliocene to Recent of the northeastern Atlantic; and others. In addition, Tembrock included the Pliocene to early Pleistocene Japanese *Searlesia japonica* Yokoyama, 1926, and *S. decessor* Yokoyama, 1928, here regarded as belonging to the new genus *Lirabuccinum* (see below); *Ancistrolepis clarki* Tegland, 1933, from the Oligocene Blakeley Formation of Washington, which is usually assigned to *Ancistrolepis* Dall, 1895 [type species: *A. eucosmius* (Dall, 1891)] or a related genus (see MOORE, 1984; GLADENKOV *et al.*, 1988); and some middle to late Miocene species related to *Sipho gregarius* Philippi, 1846, here tentatively assigned to *Colus* Röding, 1798 [type species: *C. islandicus* (Mohr, 1786)]. All these gastropods have a small first whorl followed by a variable number of whorls with a trellislike sculpture composed of spiral and axial elements (TEMBROCK, 1968). The axial sculpture typically appears a little later than do the spiral cords, and may be absent in some species. Adults of the various species differ greatly in size, sculpture, and length of the siphonal canal. American species of *Scalaspira* have strong spiral cords that form nodes where they cross the narrow axial folds, and have a sharply recurved siphonal canal. Species of *Mohnia* have thin narrow spiral threads and, like members of the *C. gregarius* complex, lack axial sculpture. *Pirgos* shares with *Aquilofusus* the strong spiral cords that form small nodes where they cross the numerous axial ribs. I agree with TEMBROCK (1968) that *Pirgos* and *Aquilofusus* are very closely related. A review of all taxa considered by Tembrock to belong to *Scalaspira* is beyond the scope of this paper, but I suspect that several genus-level groups are involved, of which *Pirgos* (including the subjective junior synonym *Aquilofusus*) is one. Because the protoconch and early teleoconch whorls of *Searlesia* remain unknown, the relationship of that group to the *Scalaspira* complex cannot be assessed. It is noteworthy, however, that all species of *Searlesia* (except perhaps *S. forbesi*) and all of Tembrock's

Scalaspira (except for two Japanese species here assigned to *Lirabuccinum*) have the outer lip smooth within.

Another related genus is *Euthria* Gray 1850. The Recent Mediterranean species *E. cornea* (Linnaeus, 1758), which is the type species of the genus, lacks apertural lirae, as do several Miocene and Pliocene species from southern Europe. The adult outer lip is thickened and reflected, as in *Searlesia*, but the spiral sculpture is typically very fine and the axial sculpture generally consists of narrow ribs that often become obsolete on later whorls. *Buccinulum* Deshayes, 1830, is often regarded as at most subgenerically distinct from *Euthria* (PONDER, 1971). Most of the Australian and New Zealand species of *Buccinulum*, including its type species *B. lineum* (Martyn, 1784), have a lirate aperture (see below).

In summary, *Searlesia* is a European genus with a range of early Oligocene to late Pliocene, with a gap in the record in the middle and late Miocene. I regard *Searlesia* as distinct from, but perhaps related to, *Pirgos* and perhaps other taxa in Tembrock's broadly conceived version of *Scalaspira*.

Genus *Lirabuccinum* Vermeij, gen. nov.

Type species: *Buccinum dirum* Reeve, 1846.

Diagnosis: Shell fusiform, spire approximately half the total shell height; spiral sculpture of fine threads, increasing in width toward base; threads override wide, rounded, low, often slightly oblique axial folds that extend suture to suture in the spire whorls; on body whorl, axials fade out toward base; axials often obsolete on part or all of body whorl; outer lip simple, neither thickened nor reflected, lirate within, the number of lirae corresponding with the number of external spiral threads; siphonal protuberance short, deflected slightly to left, slightly recurved dorsally, not distinctly set off from rest of shell; inner lip smooth, with single weak basal fold.

Composition and comparisons: In shape and sculpture, *Lirabuccinum* (Figure 1C, D) closely resembles *Searlesia* (Figure 1A, B), such that it is easy to see why Dall and others have considered the European fossil species and the North Pacific species to belong to the same genus. Both have fusiform shells with broad axial folds and fine spiral threads. This combination of traits is, however, widespread in the Buccinidae and in related families, and is by itself hardly diagnostic.

Lirabuccinum differs from *Searlesia* in at least four ways. The inner surface of the outer lip in *Lirabuccinum* is lirate, whereas in *Searlesia* it is smooth. The outer lip in *Lirabuccinum* is thin and unreflected, whereas in adult *Searlesia* it is thickened or somewhat reflected. In *Lirabuccinum*, the siphonal canal is short and slightly twisted to the left, as well as dorsally deflected; in *Searlesia*, it is straight and not recurved. Finally, the axial folds of *Lirabuccinum* are broader and somewhat more oblique in orientation than are the orthocline, more sharply rounded axials of *Searlesia*.

Another genus that is morphologically similar to *Lira-*

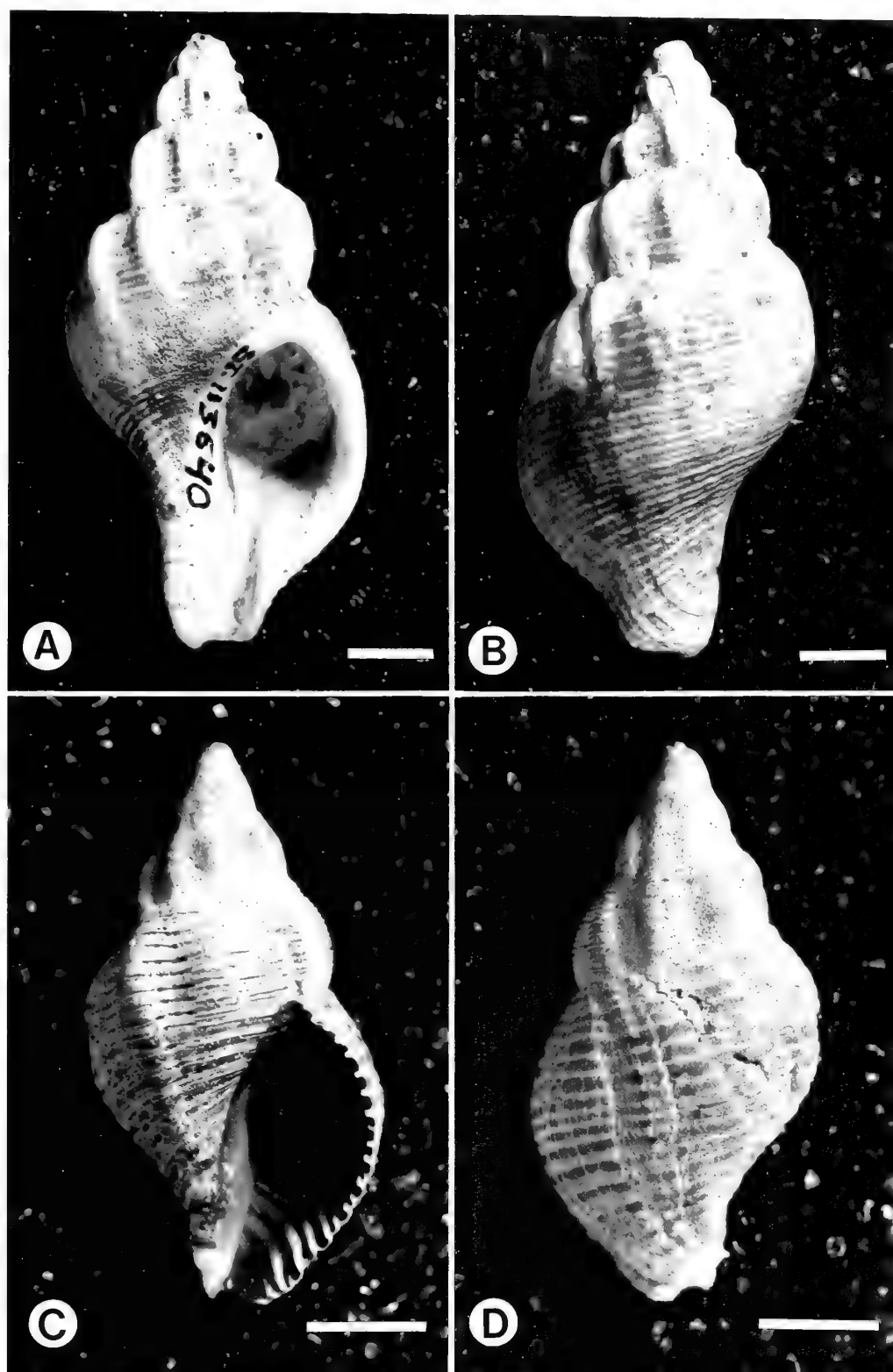


Figure 1

A and B. *Searlesia costifera* (Wood, 1848), Ellewoudsdijk, Zeeland, Netherlands, beach drift (NMNH); apertural and dorsal views. C and D. *Lirabuccinum dira* (Reeve, 1846), Whiffen Spit, Sooke, Vancouver Island, British Columbia (Vermeij collection); apertural and dorsal views. Scale bar: 1 cm.

buccinum is *Calicantharus* Clark, 1938 [type species: *C. fortis* (Carpenter, 1866)], known from the Paleocene or Eocene to the Pleistocene of western North America. Species of *Calicantharus* differ from *Lirabuccinum* by the presence of a concave area below the suture on the body whorl, an angulation or rounded swelling on the body whorl below this concave area, the smooth rather than lirate inner surface of the outer lip, and by the axial sculpture, which is expressed as axially elongated knobs or nodes rather than as continuous axial folds as in *Lirabuccinum*.

ADDICOTT (1970) assigned *Turris carlsoni* Anderson & Martin, 1914, which was included in *Searlesia* by ADEGOKE (1969) and questionably in that genus by MOORE (1963), to *Calicantharus*. This species, which occurs in the Miocene Astoria Formation of Oregon, has a concave subsutural area, a swelling below this concave area, and axial sculpture usually consisting of nodes that are most prominent on the swelling. The aperture of most specimens cannot be inspected because of the presence of matrix, but some broken specimens in the collections at UCB reveal a smooth interior. The assignment of *T. carlsoni* to *Calicantharus* therefore seems reasonable.

I disagree with ADDICOTT (1970) that *Searlesia dira* Etherington, 1931, from the Astoria Formation of Grays Harbor, Washington, is a dwarf or juvenile form of *Calicantharus kernensis* (Anderson & Martin, 1914). Etherington's taxon closely resembles the living *Lirabuccinum dirum* in sculpture. Although the apertures of both the holotype and paratype at UCB are filled with matrix, the holotype shows distinct crenulations on the outer lip, indicating the presence of internal lirae. The whorls are evenly convex, and the distinct subsutural concavity is lacking despite ETHERINGTON's (1931) claim to the contrary. I therefore agree with ETHERINGTON (1931) that this taxon is very close to the living *L. dirum*, and I place it in *Lirabuccinum*. *Calicantharus kernensis* from the Jewett Sand (early Miocene) of California is a typical *Calicantharus* with a smooth outer lip, subsutural concave area, and weakly developed nodes.

WOODRING & BRAMLETTE (1950) considered *Chrysodomus portolaensis* Arnold, 1908, from the upper Etchegoin and lower Purisima Formations of the Pliocene of California, as a species of *Calicantharus*. Inspection of the holotype at the USNM and of several lots at CAS, however, revealed that the axial sculpture (though absent on the body whorl) is expressed as continuous if bulging folds in the spire whorls, and that the inner surface of the outer lip is lirate. I therefore agree with GRANT & GALE (1931) in placing this species in their *Searlesia* (= *Lirabuccinum* herein).

Several other fossil species from the northeastern Pacific have been allocated to *Searlesia* by previous authors. *Searlesia dira* Clark, 1918, from the San Ramon Sandstone (Oligocene) of California, and *S. branneri* Clark & Arnold, 1923, from the Sooke Formation (early Miocene) of British Columbia, have regularly convex whorls and continuous axial folds disposed somewhat obliquely on the body whorl.

Although the aperture cannot be observed in the available specimens at UCB, assignment to *Lirabuccinum* is plausible. MOORE (1963) suggested that *Turris cammani* Dall, 1909, and *T. coosensis* Dall, 1909, both from the Empire Formation (late Miocene) of Oregon, belong to *Searlesia*. *Turris cammani* has a distinct posterior notch and lacks axial sculpture; it does not appear to be a buccinid. *Turris coosensis* lacks a posterior notch and possesses axial folds overridden by about 18 strong spiral threads separated by narrow grooves, but the holotype (the only available specimen at USNM) is missing the spire and the anterior canal, and its aperture is filled with matrix. This species may belong to *Lirabuccinum*, but I prefer to regard it as taxonomically indeterminable. *Searlesia olympicensis* Durham, 1944, from the Quimper Sandstone (Oligocene) of Washington, has a very short spire and differs from all species of *Lirabuccinum* by lacking axial sculpture. The apertural features of the unique holotype at UCB cannot be observed, but the absence of axial sculpture and the very short spire place this fossil outside the limits of *Lirabuccinum* as here defined.

In the western Pacific, seven taxa have been assigned by previous authors to *Searlesia*. *Fusus modestus* Gould, 1846, and its subspecies *fuscolabiata* (Smith, 1875) resemble small *Lirabuccinum dirum* in form and in having unusually strong axial folds. *Searlesia constricta* Dall, 1918 (Recent, Korea) and *Fusus coreanicus* Smith, 1875 (warm-temperate western Pacific) are superficially similar to *L. modestum* and may well belong to a single somewhat variable Recent species. Fossil taxa described as *Searlesia* from the western Pacific include *S. japonica* Yokoyama, 1926, and *S. decessor* Yokoyama, 1928, from the Pliocene of Japan, and *S. kavranensis* Sinelnikova in Gladenkov *et al.*, 1984, from the Ilinsk Suite (middle Miocene) of Kamchatka. All these species have a lirate outer lip and possess axial folds, and therefore appear to belong to *Lirabuccinum*. AMANO (1983) has, in addition, pointed to an unidentified species from the Togeshita Formation (early Miocene) of Hokkaido. Finally, *Searlesia iljinensis* Sinelnikova in Gladenkov *et al.*, 1984, from the Ilinsk Suite of Kamchatka, was excluded by GLADENKOV *et al.* (1988) from *Searlesia* (= *Lirabuccinum* of this paper) on account of its smooth outer lip. GLADENKOV *et al.* (1988) place *S. iljinensis* in *Plicifusus* Dall, 1902 [type species: *P. kroeyeri* (Möller, 1842)].

It is likely that many of these names are synonyms of one or a few somewhat variable species, because the purported differences are not great. *Searlesia kavranensis* is said to have less regular spiral sculpture and a shorter spire than the approximately coeval *Lirabuccinum branneri* (see GLADENKOV *et al.*, 1984). The expression of spiral sculpture, however, may depend on the shell's state of preservation. YOKOYAMA (1926), for example, pointed out that the spiral ribs on slightly eroded specimens of *L. japonicum* have a tripartite appearance not seen in well-preserved shells. *Lirabuccinum branneri* was said by CLARK & ARNOLD (1923) to differ from *L. dirum* in that the axial

folds extend onto the body whorl, whereas in *L. dirum* and in *L. portolaense* they are confined mainly or entirely to the spire whorls. As in other axially sculptured buccinids and related groups, there is considerable intrapopulational variation in the expression of axial sculpture in *L. dirum*. Some large *L. dirum* have axial folds on the whole of the body whorl, whereas others lack folds on this part of the shell. In the northeastern Pacific, therefore, a case could be made that there is a single somewhat variable species of *Lirabuccinum* that appeared as early as the early Miocene. The number and limits of species of *Lirabuccinum* cannot be decided definitively without more extensive fossil material than is now available.

A list of the nominal species of *Lirabuccinum* is given in Table 2. The 12 taxa range in age from Oligocene to Recent in the eastern Pacific, and from early Miocene to Recent in the western Pacific.

RELATIONSHIPS AND BIOGEOGRAPHY

We are still far from an evolutionary understanding of the Buccinidae and related families. This is well reflected in uncertainties surrounding the scope and limits of the family (PONDER & WARÉN, 1988) and in the difficulties of assigning many deep-sea species to family units (BOUCHET & WARÉN, 1986). My purpose here is to review the taxonomic distribution within the Buccinidae of some of the characters that distinguish *Searlesia* from *Lirabuccinum*, and to consider the biogeographical implications of these differences.

Lirabuccinum is one of only two genera of cool-water northern Buccinidae with a lirate outer lip. The other genus is the northwestern Pacific *Barbitonia* Dall, 1916 [type species: *B. arthritica* (Bernardi, 1858)], ranging in age from Miocene to Recent. This taxon has traditionally been regarded as a subgenus of *Neptunea* Röding, 1798 [type species: *N. antiqua* (Linnaeus, 1758)] (see DALL, 1916, 1918; HABE & SATO, 1973; GORYACHEV, 1987). NELSON (1978), however, concluded on the basis of shell microstructure that *Barbitonia* is not closely allied to *Neptunea*, but instead belongs to the group that POWELL (1951) referred to as the Buccinulidae, and that others regard as at most a subfamilial unit Buccinulinae. The Buccinulinae includes many tropical species as well as the majority of cool-water Southern-Hemisphere buccinids. Among the genera included in this group are *Buccinulum* Deshayes, 1830 [type species: *B. lineum* (Martyn, 1784)] from the late Oligocene or early Miocene to the Recent of New Zealand and Australia (PONDER, 1971; BEU & MAXWELL, 1990); *Siphonalia* A. Adams, 1963 [type species: *S. cassidariaeformis* (Reeve, 1846)] from the Eocene to the Recent of east Asia (RUTH, 1942; GLADENKOV *et al.*, 1988); *Kelletia* Fischer, 1884 [type species: *K. kelletii* (Forbes, 1850)] from the Paleocene to the Recent of the eastern Pacific (RUTH, 1942); *Penion* Fischer, 1884 [type species: *P. dilatatus* Quoy & Gaimard, 1833] and related genera, from the Paleocene to the Recent of New Zealand and Australia

Table 2

List of the nominal species of *Lirabuccinum*.

<i>L. dirum</i> (Reeve, 1846) (type): Pleistocene to Recent, northeastern Pacific.
<i>L. branneri</i> (Clark & Arnold, 1923): early Miocene (Sooke Formation, British Columbia).
<i>L. constrictum</i> (Dall, 1918): Recent, Korea.
<i>L. coreanicum</i> (Smith, 1875): Pliocene to Recent, East Asia.
<i>L. dalli</i> (Clark, 1918): Oligocene (San Ramon Sandstone, California).
<i>L. dirum miocenicum</i> (Etherington, 1931): late Miocene (Empire Formation, Washington).
<i>L. decessor</i> (Yokoyama, 1928): Miocene (Moriya Formation) Pliocene or early Pleistocene.
<i>L. japonicum</i> (Yokoyama, 1926): Pliocene or early Pleistocene (Sawane and Omma formations).
<i>L. kavranense</i> (Sinelnikova in Gladenkov <i>et al.</i> , 1984): early Middle Miocene (Ilinsk Suite, Kamchatka).
<i>L. modestum</i> (Gould, 1846): Pliocene or early Pleistocene to Recent, Japan.
<i>L. portolaense</i> (Arnold, 1908): Pliocene (Etchegoin and Purisima formations, California).
<i>L. sp. of Amano</i> , 1983: early Miocene (Togeshita Formation, Hokkaido).

(PONDER, 1973; BEU & MAXWELL, 1990); *Lirabuccinum*, from the Oligocene to the Recent of the North Pacific; and the North Atlantic genera in the complex of *Scalaspira*, *Searlesia*, and *Euthria*. POWELL (1951) further includes in his Buccinulidae almost all other cool-water Southern-Hemisphere buccinids. Lirae occur in *Buccinulum*, *Siphonalia*, *Kelletia*, *Penion*, and *Lirabuccinum*, among others, but not in the Atlantic complex discussed above under *Searlesia*, nor in most cold southern forms. With a few exceptions, "buccinulid" genera are constant with respect to the presence or absence of lirae. The exceptions occur in the tropical deep-sea genera *Manaria* Smith, 1906 [type species: *M. thurstoni* Smith, 1906], most of whose species are lirate, and *Eosipho* Thiele, 1929 [type species: *E. smithi* (Schepman, 1911)], most of which lack lirae (see BOUCHET & WARÉN, 1986). Generic assignments in *Manaria* and *Eosipho* were regarded by BOUCHET & WARÉN (1986) as tentative. Although a close relationship may exist between lirate and nonlirate genera, such as *Buccinulum* and *Euthria* (PONDER, 1971), it is possible that the lirate condition was stable once it evolved. Such a scenario could, for example, support PONDER's (1973) contention that the lirate *Penion* and *Kelletia* are closely related, and support POWELL's (1951) hypothesis that *Searlesia dira* (= *Lirabuccinum*) is derived from a Southern-Hemisphere stock perhaps related to *Buccinulum*. Alternatively, there could be a link between *Lirabuccinum* and *Siphonalia*. Until we know more about phylogenetic relationships within the Buccinidae, nothing definitive can be said about how closely related *Lirabuccinum* is to *Searlesia*. However, given that several morphologically similar lirate groups occurred in the Pacific before the time of origin of *Lirabuccinum*, and

that many nonlirate taxa from which *Searlesia* could be derived were present in the Atlantic at or before the time of origin of *Searlesia*, I suggest that *Lirabuccinum* and *Searlesia* evolved independently within their respective oceans. Similarly, it is unnecessary to link the smooth-lipped eastern Pacific *Calicantharus* and *Eosiphonalia* Ruth, 1942 [type species: *E. washingtonensis* (Weaver, 1916); Paleogene of Washington, Oregon, and California] with *Lirabuccinum*.

Given the far-reaching similarity in form and sculpture between European and North Pacific species previously included in *Searlesia*, some investigators might elect to perpetuate the *status quo* notwithstanding the small but consistent differences between *Searlesia* s.s. and the new genus *Lirabuccinum*. If this course were followed, however, the name of the inclusive genus could not be *Searlesia* because, as argued above, the immediate likely ancestors of the Pacific and Atlantic groups are best allocated to such genera as *Buccinulum*, *Siphonalia*, and *Euthria*. If *Searlesia* s.s. arose from *Euthria*-like ancestors with a nonlirate aperture, and if *Lirabuccinum* came from a lirate *Buccinulum*-like group, one could unite the Pacific and Atlantic branches in *Buccinulum* s.l., of which *Euthria* would be a distinct subgenus. The precise choice of names is, I believe, less important than the argument that the North Pacific and North Atlantic species previously brought together under *Searlesia* represent two independent lineages. The establishment of the genus-level taxon *Lirabuccinum* more accurately reflects this hypothesis of independent descent than do other possible schemes of classification.

The clarification of the relationships and taxonomy of *Searlesia* and *Lirabuccinum* is of more than routine biogeographical interest. As conceived by DALL (1916, 1918) and most other authors, *Searlesia* had representatives in both the North Pacific and North Atlantic oceans. Given that *Searlesia* in Europe was known only from the Pliocene and that *Searlesia* in the Pacific was soon discovered to extend back to the Miocene and Oligocene, *Searlesia* has been regarded as an invader from the Pacific to the Atlantic via the Arctic (DAVIES, 1929; DURHAM & MACNEIL, 1967; VERMEIJ, 1989). The reinterpretation advocated here radically revises this biogeographical history. Neither the true Atlantic *Searlesia* nor the convergent Pacific *Lirabuccinum* participated in the trans-Arctic interchange, and there was no geographical restriction of *Searlesia* to the Pacific as VERMEIJ (1989) inferred. Instead, the two groups evolved independently and remained confined to the Pacific and Atlantic basins. Both groups can be traced back to the Oligocene. *Searlesia* apparently became extinct at the end of the Pliocene in Europe, whereas *Lirabuccinum* is still living, being represented by vicariant species on the American and Asian sides of the temperate North Pacific.

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Four New Species and a New Genus of Opisthobranch Gastropods from the Pacific Coast of North America

by

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Abstract. This paper describes four new species of opisthobranchs from the eastern Pacific. *Runcina macfarlandi* is described from Oregon and may also be known as far south as Monterey Bay, California. *Baptodoris mimetica* is known from Monterey Bay, south to Isla San Martín, Baja California. This represents the first record of the genus from eastern Pacific waters. *Noumeaella rubrofasciata* is described from southern California south to Islas San Benitos, Baja California. *Anetarca* gen. nov., with type species *A. armata*, is described from the Pacific coast of central Baja California.

INTRODUCTION

The opisthobranch fauna of the Pacific coast of North America has been well studied (MACFARLAND, 1966; BEHRENS, 1980; McDONALD & NYBAKKEN, 1980; McDONALD, 1983). Despite the fact that the fauna has been extensively surveyed, additional species continue to be described (MILLEN, 1986, 1987; GOSLINER & BEHRENS, 1986; BEHRENS, 1987; BEHRENS & GOSLINER, 1988a, b; GOSLINER & BERTSCH, 1988). Additional recent collections continue to yield undescribed species. This paper describes four additional species of opisthobranchs from the eastern Pacific. All four of these species are placed in genera that have no previously described representatives recorded from the eastern Pacific. The systematic relationships and biogeographical affinities of these species are discussed.

SPECIES DESCRIPTIONS

Order Cephalaspidea

Family RUNCINIDAE H. & A. Adams, 1854

Genus *Runcina* Forbes & Hanley, 1853

Runcina macfarlandi Gosliner, sp. nov.

(Figures 1A, 2, 3)

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 074572, found on submerged tips of *Cladophora trichotoma* (C. A. Agardh) Kützing, in

high intertidal pools, Seal Rock State Park, Seal Rock, Lincoln County, Oregon, 9 July 1990, Cynthia Trowbridge. Paratype, dissected, CASIZ 074573, same date and locality as holotype. Paratype, CASIZ 074574, dissected, same locality as holotype, 20 June 1990, Cynthia Trowbridge.

Distribution: *Runcina macfarlandi* has been collected from two localities within Lincoln County Oregon (Cynthia Trowbridge, personal communication), Boiler Bay State Park, north of Depoe Bay, south to Seal Beach State Park, near Seal Beach. This species probably has also been collected from the central California coast (see Discussion).

Etymology: This species is named for the late Frank Mace MacFarland, who pioneered studies of eastern Pacific opisthobranchs. He also first illustrated a specimen of a species of *Runcina* collected from Pacific Grove in 1899. In all probability this is the species described here.

External morphology: Living animals (Figures 1A, 2A) are 3–5 mm in length. The notum is yellowish brown with darker brown to black pigment in the central portion of the body. The head shield is flattened anteriorly and widens into the broad ovoid body. Posteriorly the ctenidium consists of two simple, rounded plicae, which are well separated from each other. The eyes are visible along the anterolateral sides of the body, between the notum and the foot. A sperm groove traverses the right side of the body from the hermaphroditic gonopore near the posterior end to the penial aperture on the anterolateral end of the body.

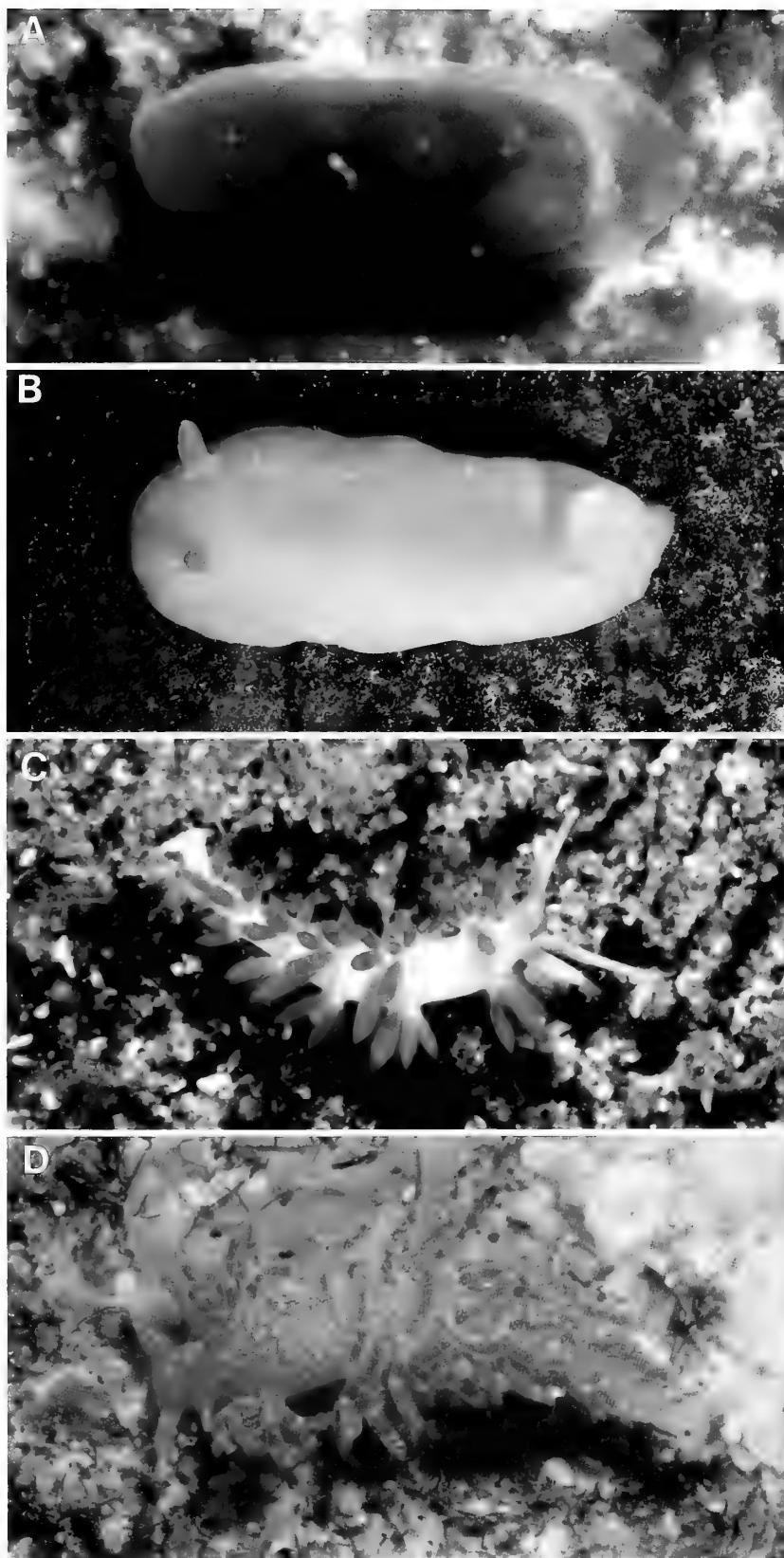


Figure 1

Living animals. A. *Runcina macfarlandi* sp. nov. B. *Baptodoris mimetica* sp. nov. C. *Noumeaella rubrofasciata* sp. nov. D. *Anetarca armata* gen. et sp. nov.

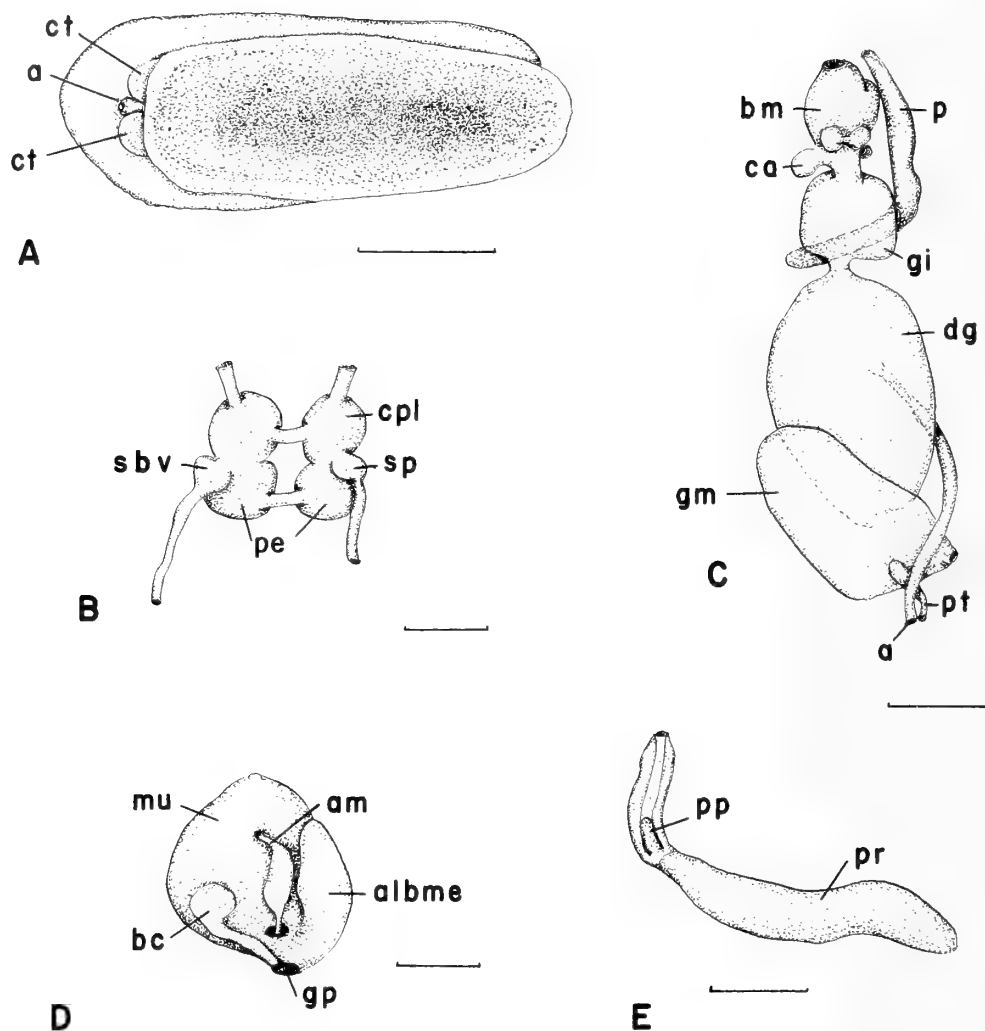


Figure 2

Runcina macfarlandi sp. nov. A. Dorsal view of living animal: a, anus; ct, ctenidium; scale = 1 mm. B. Central nervous system: cpl, cerebral pleural ganglion; pe, pedal ganglia; sbv, subintestinal-visceral ganglion; sp, suprainsintestinal ganglion; scale = 0.25 mm. C. Digestive tract: a, anus; bm, buccal mass; ca, caecum; dg, digestive gland; gi, gizzard; gm, genital mass; p, penis; pt, ptalyne gland; scale = 0.5 mm. D. Reproductive system: albme, albumen-membrane glands; am, ampulla; bc, bursa copulatrix; gp, genital pore; mu, mucous gland; scale = 0.25 mm. E. Penis: pp, penial papilla; pr, prostate; scale = 0.25 mm.

Digestive tract (Figure 2C): The buccal mass is short and muscular. Within the mass, near its anterior end is a thin labial cuticle that had no obvious chitinous jaw rodlets. More posterior is the radula (Figure 3A) with a formula of $19-21 \times 1 \cdot 1 \cdot 1 \cdot$, in two specimens examined. The rachidian teeth (Figure 3B) are broad, with a pair of elongate, posteriorly directed limbs. The masticatory edge contains a pair of rounded, denticulate pads on either side of the small central denticle. Each of these rounded cutting surfaces bears 5-11 elongate denticles. The lateral teeth (Figure 3C) are elongate and curved. The masticatory border is entirely smooth, without any trace of denticles.

Posterior to the buccal mass, the esophagus narrows and contains a large, saccate caecum. The posterior end of the esophagus enters the muscular gizzard. The gizzard is larger than the buccal mass. Four longitudinally directed gizzard plates are contained within the gizzard. Each chitinous plate (Figure 3D) contains 6 or 7 denticulate transverse ridges.

Posteriorly, the gizzard is connected to the large, lobate digestive gland. From the digestive gland, a narrow intestine emerges and empties into the anus at the posteromedial end of the body. A simple ptalyne gland is present adjacent to the intestine and exits into the anus.

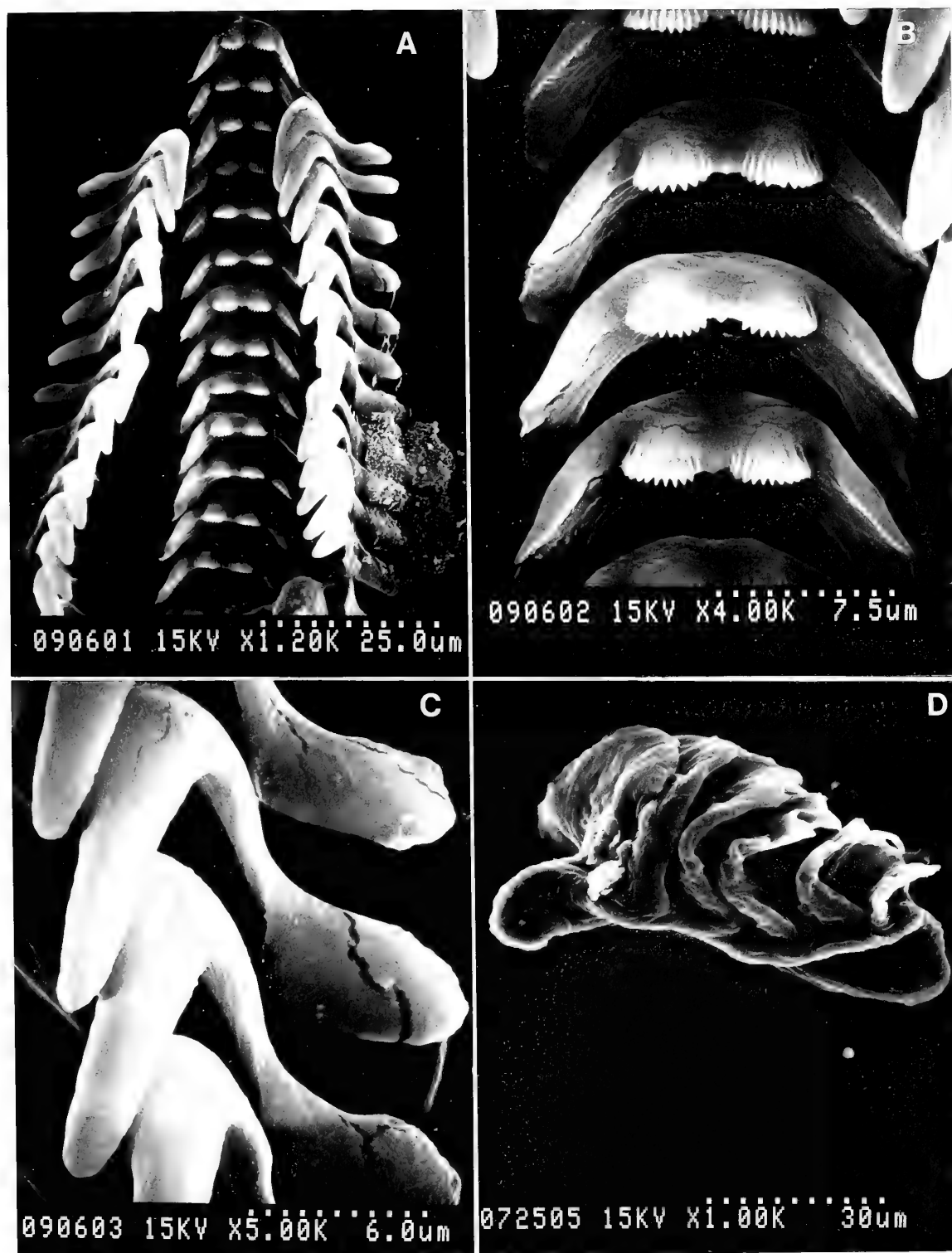


Figure 3

Runcina macfarlandi sp. nov. Scanning electron micrographs. A. Entire width of radula. B. Rachidian teeth. C. Lateral teeth. D. Gizzard plate.

Table 1
Morphological variation in the Runcinidae.

Genus	Shell	Gill	Radular formula	Rachidian	Laterals	Gizzard
<i>Runcina</i> Forbes, 1851	present or absent	2 or 3, right side	1.1.1.	denticulate	denticulate or smooth	present
<i>Ildica</i> Bergh, 1889	present, external	plicate, right side	1.1.1.	smooth	smooth	present
<i>Metaruncina</i> Baba, 1967	present	plicate, right side	reduced	reduced	reduced	present
<i>Runnica</i> Miller & Rudman, 1968	present	plicate, right side	1.1.1.	denticulate	short, smooth	present
<i>Runcinella</i> Odhner, 1924	absent	5 circular plicae	2.1.2.	denticulate	outers bifid	present
<i>Runcinida</i> Burn, 1963	absent	5 linear plicae	1.1.1.	denticulate	smooth	present
<i>Ilbia</i> Burn, 1963	absent	absent	1.1.1.	trifid	denticulate	absent
<i>Pseudoilbia</i> Miller & Rudman, 1968	absent	absent	2.0.2.	absent	unequal, denticulate	absent
<i>Lapinura</i> Marcus & Marcus, 1970	present, external	plicate, right side	1.1.1.	denticulate	smooth	present

Central nervous system (Figure 2B): The central system surrounds the esophagus, posterior to the buccal mass. The highly cephalized system is formed of four distinct ganglia. A pair of large cerebral ganglia are separated by a short cerebral commissure. The paired pedal ganglia are situated below the esophagus and are separated from each other by a short commissure. On the left side of the nerve ring is a smaller ganglion representing the fusion of the left pleural and suprainestinal ganglia. On the right side, the right pleural ganglion, suprainestinal, and visceral ganglia have fused to form another small ganglion. No distinct visceral loop was observed.

Reproductive system (Figure 2D): The reproductive system is monaulic. The short saccate ampulla narrows and enters the female gland mass between the mucous and albumen glands. The female glands exist at the gonopore adjacent to the duct of the spherical bursa copulatrix.

The penis (Figure 2E) is thin and elongate. The posterior end curves under the ventral surface of the gizzard. The posterior three-fourths of the penis is composed of the indistinct prostate and spermatic bulb. The penis proper consists of a simple, poorly developed papilla, which is devoid of any armature.

Discussion: The Runcinidae have been subdivided into as many as nine genera by various authors (Table 1). These genera are separated largely on the basis of differences in the arrangement and structure of the ctenidium, formula and shape of the radular teeth, and presence or absence of a shell and gizzard plates. Other than *Runcina*, all other genera contain only a single species. CLARK (1984) considers *Lapinura* Er. Marcus & Ev. Marcus, 1970, as a junior synonym of *Runcina*. THOMPSON & BRODIE (1988) considered *Runnica* Miller & Rudman, 1968, to be a junior synonym of *Runcina*. Based on this synonymy, they considered *Runcina* to include 14 nominal species. GOSLINER (1990) discussed problems related to the systematics of eastern Atlantic species of *Runcina* and suggested possibly synonyms. Certainly, more extensive study of the Runcinidae is required to determine the range of variability of genera and their phylogenetic relationships.

Among described runcinids, *Runcina macfarlandi* is the only species known to possess a single flattened branchial plica on either side of the anus. In other aspects of its anatomy, it does not differ markedly from other species currently placed in the genus *Runcina*. Rather than erect yet another monotypic genus, I prefer to place the present species in the genus *Runcina*. Of described species of *Runcina*, only *R. marshae* Burn, 1966, is similar to *R. macfarlandi* in having a yellow ground color. However, the rachidian teeth of *R. marshae* are not strongly bilobed, as in *R. macfarlandi*. Also the gizzard plates of *R. marshae* are more highly denticulate than in *R. macfarlandi*.

Specimens of runcinids have previously been collected from the coast of California. In MacFarland's original field notes (housed at the California Academy of Sciences), I have located an illustration of a runcinid collected from Pacific Grove on 12 August 1899. The animal is similar in color and shape to the present species. No other details of the anatomy of this animal are known and no specimens have been found in the MacFarland Collection at the California Academy of Sciences. GOSLINER & WILLIAMS in Smith & Carlton, 1975, listed a yellow *Runcina* from Pacific Grove. This record was based on specimens that Peter Glynn collected and Michael Ghiselin identified from Hopkins Marine Station. Attempts to find other material from the Monterey Peninsula have been unsuccessful to date. It is likely, however, that specimens collected from these localities are conspecific with the present species.

Order Nudibranchia

Suborder Doridacea

Family DISCODORIDAE Bergh, 1891

Genus *Baptodoris* Bergh, 1884

Baptodoris mimetica Gosliner, sp. nov.

(Figures 1B, 4-6)

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 074575, intertidal zone, Asilomar State Park, Pacific Grove, California, 6 July 1986,

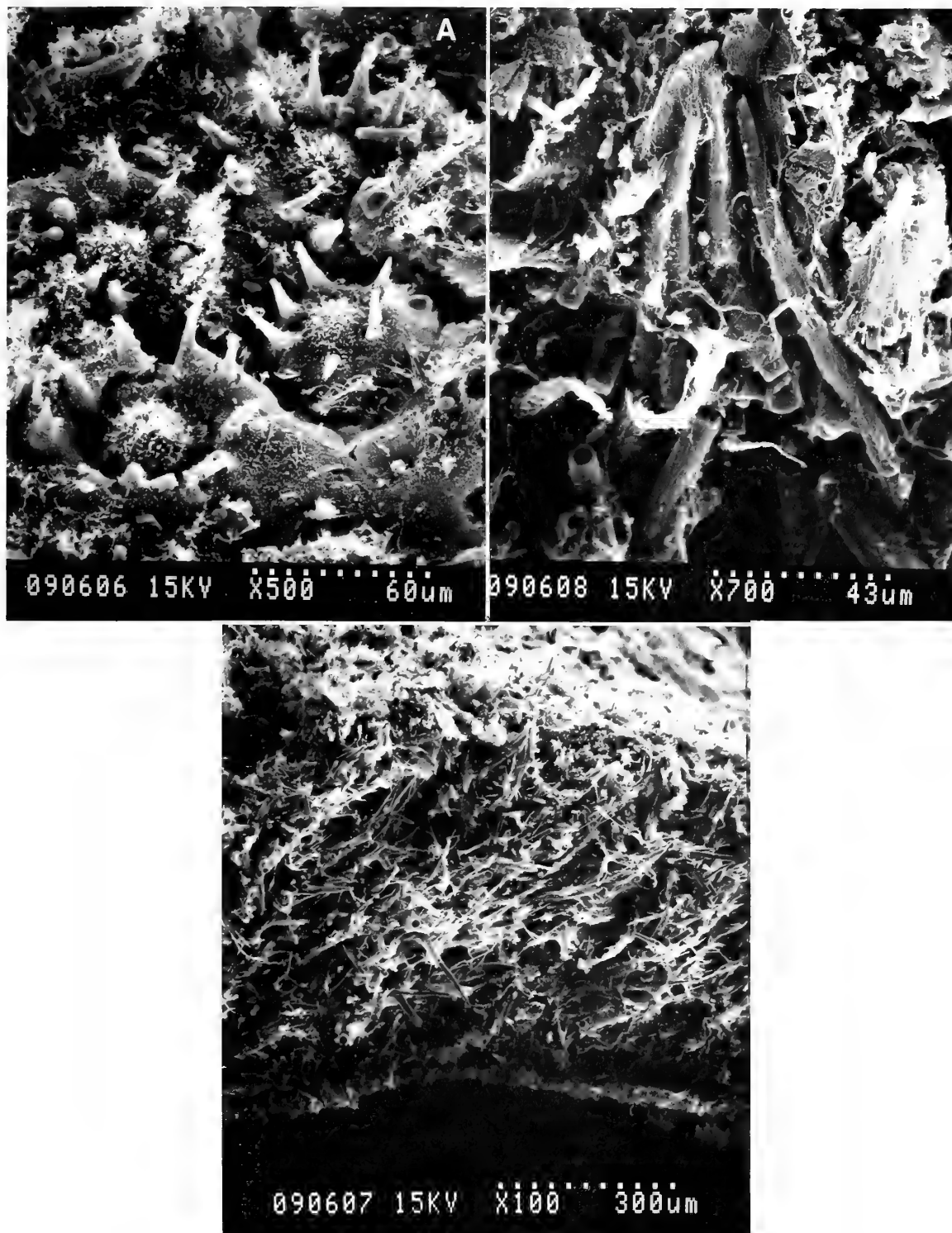


Figure 4

Baptodoris mimetica sp. nov. Scanning electron micrographs of notal structures. A. Surface view of caryophyllidia. B. Cross section of caryophyllidium. C. Cross section of notum.

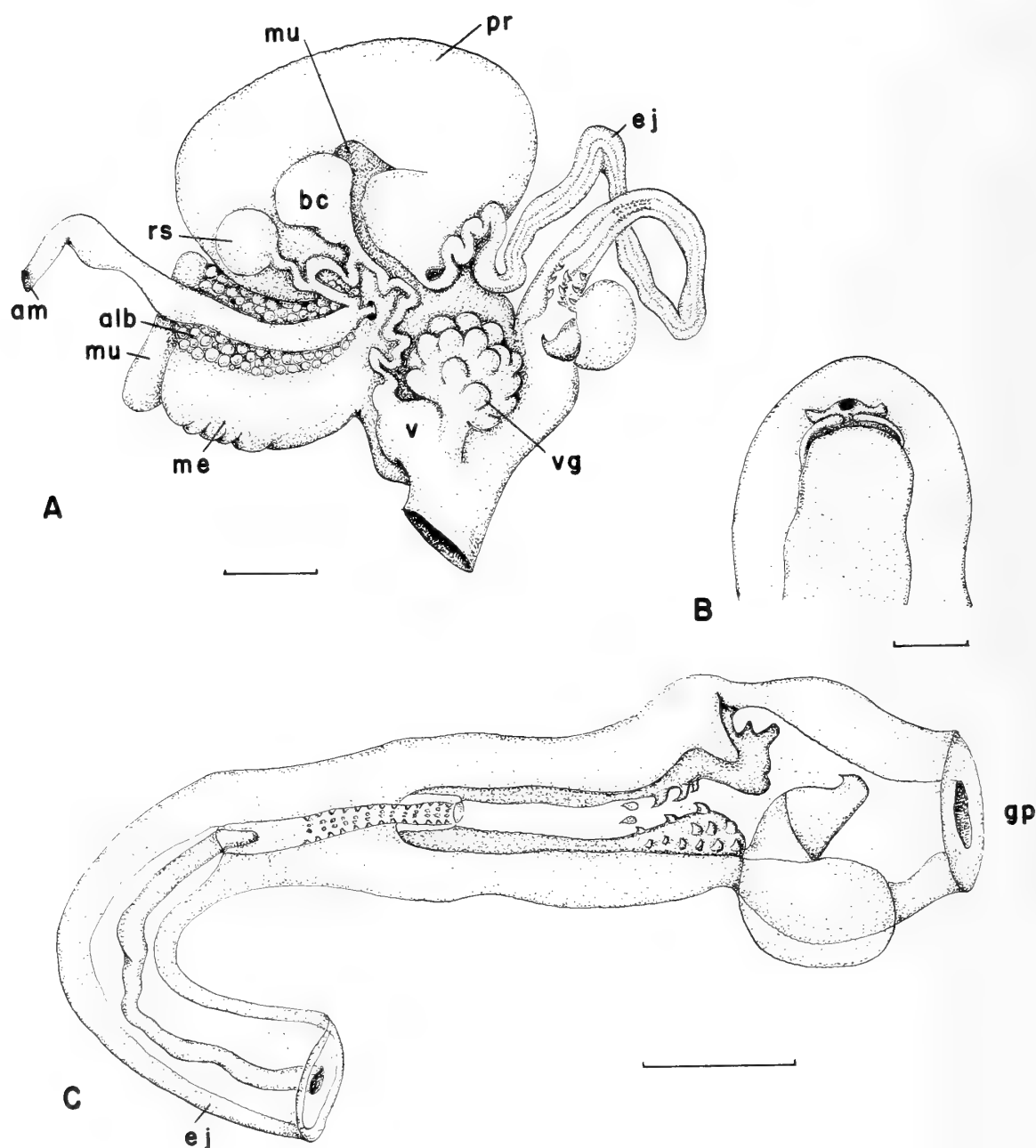


Figure 5

Baptodoris mimetica sp. nov. A. Reproductive system: alb, albumen gland; am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of vas deferens; me, membrane gland; mu, mucous gland; pr, prostatic portion of vas deferens; rs, receptaculum seminis; v, vagina; vg, vestibular gland; scale = 0.5 mm. B. Ventral view of animal showing head and anterior end of foot: scale = 3 mm. C. Distal end of vas deferens and penis: ej, ejaculatory duct; gp, gonopore; scale = 0.5 mm.

Gary McDonald. Paratypes, two specimens, CASIZ 074576, south storage tank, Long Marine Laboratory, Santa Cruz, California, 5 October 1983, G. McDonald. Paratype, dissected, CASIZ 074577, south storage tank, Long Marine Laboratory, Santa Cruz, California, 5 October 1983, G. McDonald. Paratype, dissected, CASIZ

074578, Long Marine Laboratory, Santa Cruz, California, October 1989, G. McDonald. Paratype, CASIZ 072093, Monastery Beach, Carmel, California, 5 October 1975, Andrea Purdue. Paratype, CASIZ 069142, 6 m depth, Monastery Beach, Carmel California, 6 March 1976, A. K. McDonald. Paratype, CASIZ 072094, Mon-

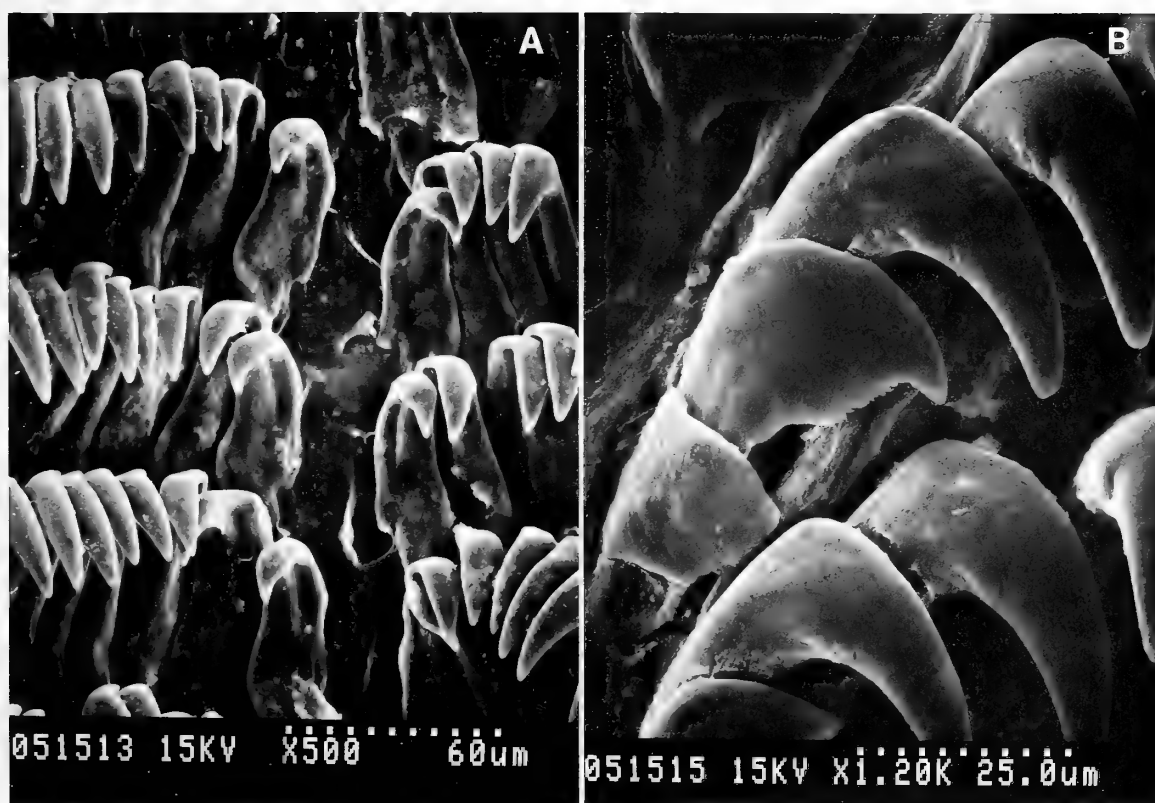


Figure 6

Baptonoris mimetica sp. nov. Scanning electron micrographs of radula. A. Innermost radular teeth. B. Outermost radular teeth.

astery Beach, Carmel, California, 25 November 1970, Ed Stark. Paratype, dissected, CASIZ 074579, Isla San Martín, Baja California, David Behrens.

Distribution: This species has been collected from Santa Cruz, California, to Isla San Martín, off the Pacific coast of Baja California, Mexico.

Etymology: The epithet *mimetica* refers to the striking external similarity between this species and the common sympatric dorid nudibranch *Doriopsilla albopunctata* (Cooper, 1863).

External morphology: The living animals (Figure 1B) reach 25 mm in length. The ground color is bright lemon yellow. Small opaque white spots are uniformly scattered over the dorsal surface of the notum. The rhinophores are uniformly brown. The gills are translucent white.

The notum is finely studded with minute caryophyllidia. When examined under the scanning electron microscope, these caryophyllidia are 30–50 μm in diameter. Each caryophyllidium (Figure 4A) is supported by a ring of 7–12 calcareous spicules. In the center is a mound covered by dense cilia. The structure of the caryophyllidia is very similar to that described by KRESS (1981) and FOALE &

WILLAN (1987) for species of *Rostanga* and *Jorunna*. The supporting spicules of the caryophyllidia penetrate deeply into the notal tissue (Figure 4B). The rigid notum contains a dense mat of calcareous spicules (Figure 4C).

The rhinophores are perfoliate with 14 closely spaced lamellae. The branchial plume consists of 7 or 8 bipinnate gills. The gills are held erectly when fully extended. The anus is situated within the center of the branchial plume. The head (Figure 5B) is well developed, with paired labial tentacles. The foot is broad, and bilabiate anteriorly. The posterior end of the foot is rounded and extends beyond the posterior limit of the notum. The genital aperture is situated between the ventral portion of the notum and the foot, approximately one-third of the body length behind the head.

Buccal mass: The buccal mass is large and muscular. The anterior portion of the mass is lined with a thick labial cuticle, which is devoid of any jaw rodlets. More posteriorly, is the radula, with a formula of $38 \times 51.0 \cdot 51 \cdot$ and $41 \times 52.0 \cdot 52 \cdot$ in two specimens observed. The rachis lacks a rachidian row of teeth. The inner lateral teeth (Figure 6A) are simply hamate. They are devoid of any denticles. The laterals from the middle of the half row are larger

than the inner ones and have a more elongate cusp. The outermost laterals (Figure 6B) are short and flattened, with a finely serrate masticatory border. The two teeth immediately inward from these two (Figure 6C) are typically hamate, but bear 2 or 3 denticles on their outer edge.

Reproductive system (Figure 5A, C): The arrangement of the reproductive organs is triaulic. The ampulla is elongate and slightly curved. At its distal end, the ampulla divides into a short oviduct and the vas deferens.

The oviduct is short and enters the female gland mass between the albumen and membrane glands. The mucous gland is massive with several lobes. It terminates at the nidamental opening, immediately ventral to the common atrium of the vas deferens and vagina. At the junction of the ampulla, vas deferens, and oviduct is the uterine duct. After a short distance, it branches to the duct of the spherical receptaculum seminis. The uterine duct curves and joins the base of the pyriform bursa copulatrix. From this junction the thin, convoluted vagina extends distally. At its distal end it expands into a vaginal atrium, which joins with a large lobate vestibular gland.

The vas deferens expands immediately into the massive prostate. The prostate narrows into a convoluted ejaculatory segment, which gradually widens. The muscular portion of the ejaculatory duct empties into a tubular section with a chitinous lining (Figure 5C). The proximal portion of this segment is lined with four rows of minute chitinous hooks. This area widens into a section without armature. More distally is a segment with four shorter rows of larger spines. Immediately distal to this point the duct widens markedly. On one side of the duct is a swollen muscular pouch, which bears a single large chitinous spine with a curved apex.

Discussion: The generic distinctions within the Discodorididae are the subject of considerable confusion. More than 30 genera have been included within the family by various workers (THIELE, 1931; FRANC, 1968). Many genera are monotypic and are known only from the original descriptions, which are often incomplete. Members of the family appear to be united by several apomorphic features. All species appear to have digitiform labial tentacles, an anteriorly divided foot, and a thick, well-developed prostate. Other features vary within and between genera. The notum may be composed of simple tubercles or complex caryophyllidia. Presence or absence of caryophyllidia may vary within a single genus, such as *Sclerodoris* Eliot, 1904 (RUDMAN, 1978). Jaw rodlets may be present or absent in a single genus, such as *Jorunna* Bergh, 1876 (EV. MARCUS, 1976). Outer radular teeth may be denticulate or simply hamate within a single genus, as in *Halgerda* Bergh, 1880 (RUDMAN, 1978). A vestibular gland and penial spines may be present or absent in species of *Sclerodoris* (KAY & YOUNG, 1969; RUDMAN, 1978). Many of the described genera appear to be paraphyletic or are based solely on plesiomorphic features (e.g., *Discodoris*

Bergh, 1877). Revision of the systematics of the cryptobranch dorids must await detailed evaluation of characters, their polarity and phylogeny. Until this is achieved, placement of taxa within genera must be regarded as tentative.

The present species is placed within the genus *Baptodoris* Bergh, 1884, based on its similarity to the type species, *B. cinnabarina* Bergh, 1884. The genus is characterized by having a firm, finely spiculate notum, digitiform labial tentacles, a labial cuticle without rodlets, and penial armature with numerous hooks. SCHMEKEL (1970) further described the reproductive anatomy of *B. cinnabarina*. This species has numerous rows of spines lining the distal portion of the vas deferens and has a single larger penial spine. It also has an expanded vaginal atrium with an adjacent vestibular gland.

Baptodoris mimetica differs from *B. cinnabarina* in several significant regards. The ground color of the present species is yellow rather than scarlet. The radular teeth of *B. cinnabarina* are all narrow and hamate, without denticles. In *B. mimetica* the hamate teeth are broader and the outer ones are denticulate and serrate. The penial spines of *B. mimetica* are more numerous and complex in their arrangement.

Llera & Ortea in ORTEA *et al.* (1982) described *Baptodoris perezii* from the Canary Islands and reviewed the other members of the genus. Like *B. mimetica*, *B. perezii* is yellow, but has black rather than yellowish spots. *Baptodoris perezii* has unipinnate rather than bipinnate gills. In this species, caryophyllidia are restricted to the margins of the notum rather than being evenly scattered. In *B. perezii*, the radular teeth are simply hamate, without denticles or serrations. This species also lacks a vestibular gland.

Baptodoris fongosa Risbec, 1928, known only from its original description from New Caledonia, is reddish yellow with gray patches. Its outer four teeth per half row are finely serrate, while in *B. mimetica* only the outer two teeth are serrate. A vestibular gland was not described.

Baptodoris tuberculata Bergh, 1888a, described from Thailand, is poorly known. All of its radular teeth are hamate, without denticles, except for some of the outermost teeth, which are bifid. A penial gland is present at the gonopore.

ORTEA, *et al.* (1982) also considered *Aporodoris rubra* Bergh, 1905, as a species of *Baptodoris*. In this species the outer four teeth are finely serrate.

The anatomy of *Baptodoris fongosa*, *B. tuberculata*, and *B. rubra* must be more completely described before they can be adequately compared with other described discodorids. Clearly though, enough is known about these taxa to distinguish them from *B. mimetica*.

Gargamella Bergh, 1894, contains two described and two undescribed species that share most of the features listed above for *Baptodoris cinnabarina* (see ODHNER, 1926; EV. MARCUS, 1959; GOSLINER, 1987). The only significant difference between species of this genus and those included

in *Baptodoris* is that the vestibular duct is present on the vas deferens rather than on the vaginal duct. On this basis, one might seriously question the homology of these structures. Further study is required to verify the location of these vestibular glands and to examine details of their histology and function.

Species of *Platydoris* Bergh, 1877, also have spines lining the vas deferens (KAY & YOUNG, 1969; EDMUNDS, 1971). Their vestibular gland enters the vas deferens, as in *Gargamella*, rather than entering the vagina. Externally, members of *Platydoris* differ from species of both *Baptodoris* and *Gargamella*, as they are dorsoventrally flattened and lack caryophyllidia.

Baptodoris mimetica closely resembles *Doriopsilla albopunctata* (Cooper, 1863) and other conspecific species of porostomes, whose systematic status remains unclear, in its external morphology and coloration. Living animals of the two species can be readily distinguished. *Doriopsilla albopunctata* has a soft fleshy texture, whereas *B. mimetica* is rigid and is finely covered with caryophyllidia. The gills of *D. albopunctata* are more highly pinnate and cover more of the notum when fully extended. The gills of *B. mimetica* are held more erectly than those of *D. albopunctata*. Ventrally, *B. mimetica* has elongate digitiform labial tentacles, whereas in *D. albopunctata* and other porostomes, rudimentary tentacles are present on either side of the mouth.

Suborder Aeolidacea

Family FACELINIDAE Bergh, 1889

Subfamily FAVORININAE Bergh, 1889

Genus *Noumeaella* Risbec, 1937

Noumeaella rubrofasciata Gosliner, sp. nov.

(Figures 1C, 7, 8)

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 074580, 20 m depth, S end of Isla San Benito Oeste, Baja California, 17 August 1987, T. M. Gosliner. Paratype, dissected, CASIZ 074581, same date and locality as holotype. Paratype, CASIZ 074582, same date and locality as holotype. Paratype, CASIZ 074583, Isthmus Cove, Santa Catalina Island, California, 10 October 1985, James Morin. Paratype, CASIZ 074027, under rock, 2–4 m depth, near point in front of Hotel Punta Colorada, Punta Colorada, Gulf of California, Baja California Sur, Mexico, 15 November, 1972, Antonio J. Ferreira.

Distribution: This species has been found along the California coast from Santa Barbara Island (Marc Chamberlain, personal communication) and Santa Catalina Island (present study). It has also been found from the Pacific coast of Mexico from Islas San Benitos (present study) and from Punta Colorada, Baja California Sur, in the Gulf of California (present study).

Etymology: The epithet *rubrofasciata* refers to the reddish stripe present on the middorsal portion of the head.

External morphology: The living animals (Figure 1C) reach 8 mm in length. The ground color is translucent white. Most of the dorsal and lateral surfaces of the body are covered with dense opaque white. The base and apex of the rhinophores, the basal one-fourth of the oral tentacles, and the sides and bottom of the foot are the only areas that are translucent white. A red-orange stripe extends middorsally from the anterior limit of the head to the anterior limit of the rhinophores. The base of each cerata is opaque white. Above the base, the cerata are translucent and the brick-red digestive gland is visible. The large cnidosac is deep red-orange.

The body is thin and elongate (Figure 7A). The foot is approximately equal in width to the notum and tapers to an elongate, posterior tail. The rhinophores (Figure 7B) are widest in the middle and taper to an elongate apex. Their posterior surface bears numerous, elongate papillae. The narrow and acutely pointed oral tentacles are about twice as long as the rhinophores. The anterior ends of the foot form elongate tentacles, which are sharply recurved when the animal is actively crawling. The cerata are short and somewhat inflated in appearance. They are widest in their distal third. The cnidosac is large and conical in shape. The cerata are arranged in a series of 5–7 horseshoe-shaped arches on either side of the body. The single precardiac arch contains 6–9 cerata in the four specimens examined. The first postcardiac arch contains 5–7 cerata. The subsequent arches contain fewer cerata posteriorly and are each composed of 1–6 cerata. The anus is cleio-proctic, located on the right side of the body, within the first postcardiac ceratal arch. The nephroproct is located within the interhepatic space. The gonopore is situated below the anterior limb of the anteriormost ceratal arch.

Buccal mass: The buccal mass is short and muscular. A lobate oral gland is present on either side of the buccal mass (Figure 7C). Each gland extends posteriorly for about two-thirds of the length of the buccal mass. Within the mass are the paired chitinous jaws (Figure 7D). The masticatory border of the jaw is of moderate length (Figure 8A) and bears 5 or 6 rows of irregular denticles (Figure 8B). The outermost denticles are irregularly divided into 4 or 5 apices while those of the inner 4 or 5 rows have a simple acute apex.

The radular formula in the one specimen examined was $14 \times 0.1 \cdot 0$. The radular teeth (Figure 8C, D) are broadest posteriorly. The posterior limbs of the teeth are acutely pointed and evenly arched. The central cups is narrow but wider and more elongate than the adjacent denticles. There are 7–9 elongate, inwardly curved denticles on either side of the central cusp.

Reproductive system (Figure 7E, F): The arrangement of the organs is androdiaulic. The ampulla is thin and

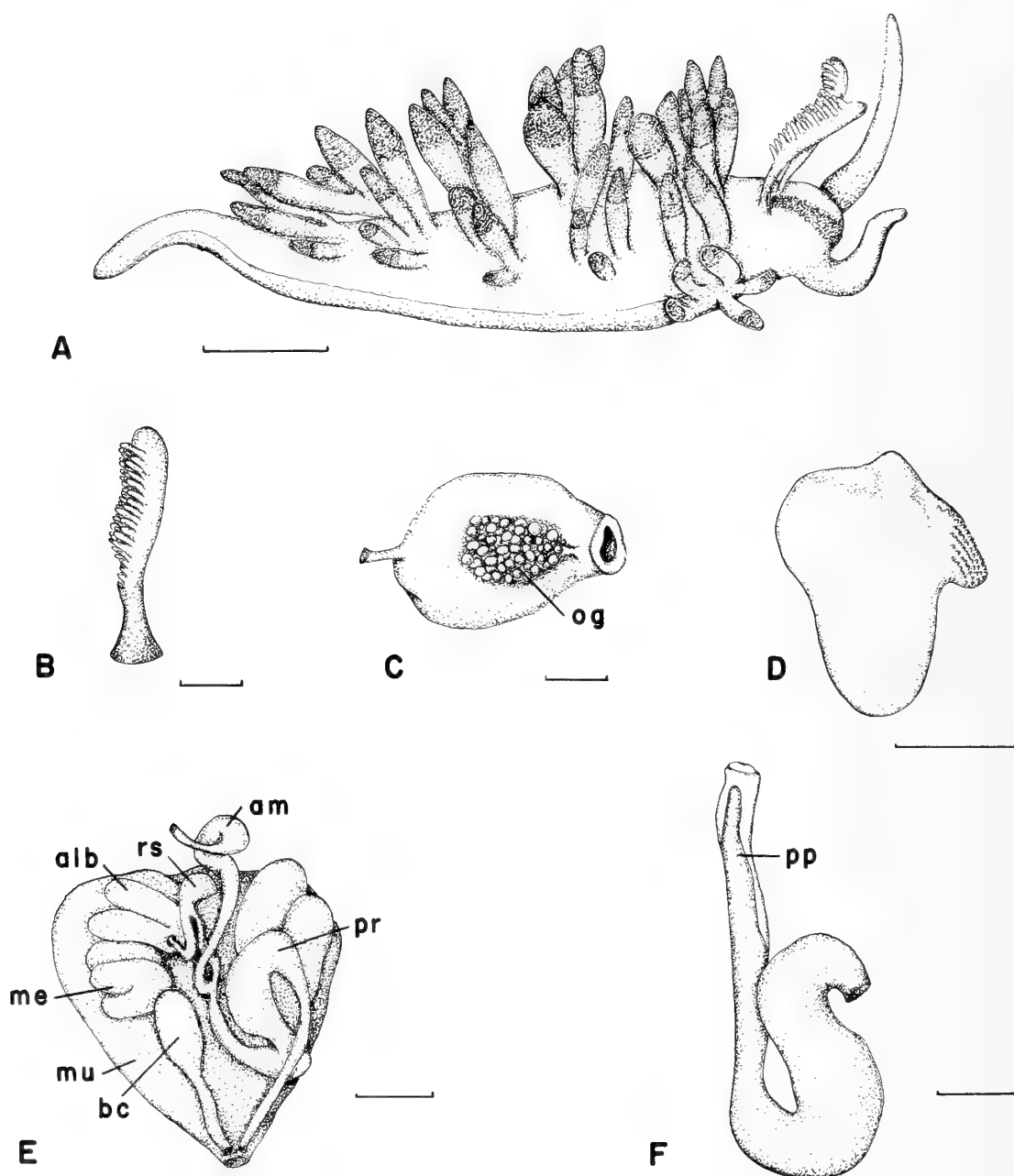


Figure 7

Noumeaella rubrofasciata sp. nov. A. Lateral view of preserved specimen: scale = 1 mm. B. Rhinophore: scale = 0.25 mm. C. Buccal mass: og, oral gland; scale = 0.25 mm. D. Jaw: scale = 0.5 mm. E. Reproductive system: alb, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; pr, prostatic portion of vas deferens; rs, receptaculum seminis; scale = 0.25 mm. F. Penis: pp, penial papilla; scale = 0.125 mm.

slightly coiled. Distally, the ampulla narrows and bifurcates into the oviduct and vas deferens. The oviduct is narrow and expands into a partially serial pyriform receptaculum seminis. The oviduct again narrows immediately before its entrance into the bilobed albumen gland.

The lobate membrane gland is adjacent to the albumen gland. The mucous gland is the largest portion of the reproductive system and consists of three major lobes. The mucous gland terminates at the common gonopore. The elongate duct of the thin-walled bursa copulatrix joins the

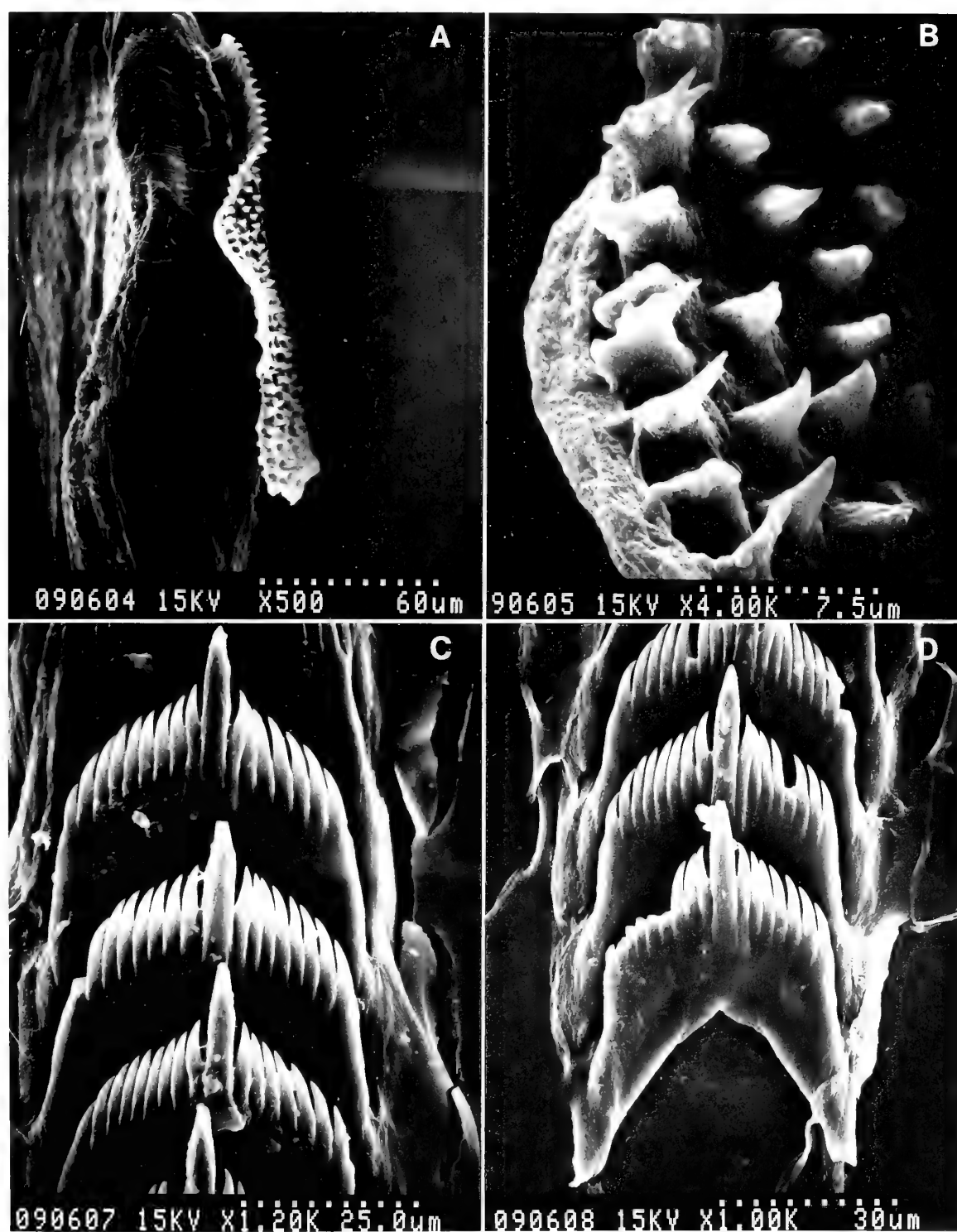


Figure 8

Noumeaella rubrofasciata sp. nov. Scanning electron micrographs. A. Masticatory border. B. Denticles of masticatory border. C and D. Radular teeth.

mucous gland near the gonopore. The vas deferens gradually expands into a curved prostatic portion, which again gradually narrows into the simple, elongate penial papilla. The papilla lacks any armature or glands.

Discussion: The present species is clearly placed within the Facelinidae and included with the Favorininae on the basis of its cleioproct anus, cerata all included in arches, and cuspidate radular teeth. Only members of three genera of favorinids—*Noumeaella* Risbec, 1937, *Palisa* Edmunds, 1964 and *Jason* Miller, 1974—include species with papillate rhinophores.

WILLAN (1987) discussed character polarities of primitive and derived features within the Facelinidae. On the basis of this discussion and the incorporation of other features not included by Willan, it is clear that *Noumeaella rubrofasciata* differs markedly from other facelinids with papillate rhinophores. *Moridilla brockii* Bergh, 1888b, differs from the present species in that all of the cerata are arranged in linear rows rather than in arches. *Jason mirabilis* Miller, 1974, has a vestigial radula consisting of only five teeth, some cerata arranged in arches with two rather than one row of cerata, and a penial papilla with apical glands. Members of the genera *Noumeaella* Risbec, 1937, and *Palisa* Edmunds, 1964, are most similar to the present species. *Noumeaella* includes four species (*N. curiosa* Risbec, 1937, *N. rehderi* Er. Marcus, 1965, *N. isa* Ev. Marcus & Er. Marcus, 1970, *N. africana* Edmunds, 1970), and all are known only from the Indo-Pacific tropics. *Palisa* contains only a single species, *P. kristenseni* (Ev. Marcus & Er. Marcus, 1963), which is considered a senior synonym of *P. papillata* Edmunds, 1964 (EDMUNDS & JUST, 1983). All of these species share several derived features: papillate rhinophores, cerata arranged in arches with only a single row, and a well-developed prostatic vas deferens. The only difference between *Noumeaella* and *Palisa* is that *P. kristenseni* has more precardiac cerata and an unarmed penis. Because both of these features of *Palisa* are plesiomorphic, there are no autapomorphies to distinguish it from *Noumeaella*. On this basis, and by the rule of priority, *Palisa* is considered a junior synonym of *Noumeaella*.

Noumeaella rubrofasciata can be readily separated from the other described species of the genus by its unique color pattern with red pigment and by several aspects of its internal anatomy. In *N. rubrofasciata* there are two plesiomorphic features not found in other members of the genus: the masticatory border of the jaw bears several rows of denticles, and a distinct distal bursa copulatrix is present adjacent to the gonopore. EDMUNDS (1970: fig. 20B) illustrated a structure called a bursa copulatrix in *N. africana*. However, this structure is contiguous with the serial receptaculum seminis along the oviduct, prior to its entrance into the female gland mass. It is, therefore, not considered to be homologous with a bursa situated at the gonopore, which is characteristic of *N. rubrofasciata* and most other opisthobranchs. *Noumeaella rubrofasciata* has

one apomorphic feature not known in other members of the genus: the gonopore is situated anterior to the precardiac ceratal arch, rather than posterior to it, as in the remaining members of the genus. The radular teeth of *N. rubrofasciata* are more similar to those of *N. africana* and *N. kristenseni*, where the lateral denticles are deeply incised.

Family FACELINIDAE

Anetarca Gosliner, gen. nov.

Diagnosis: Body with broad foot. Rhinophores smooth. Foot corners tentacular. Precardiac cerata arranged in arch containing a single row of cerata. Postcardiac cerata arranged in simple rows. Anus cleioproct, situated between first two postcardiac ceratal rows. Nephroproct situated within interhepatic space. Gonopore ventral to precardiac ceratal arch. Salivary glands simple. Oral glands dorsal. Masticatory border of jaws smooth. Radular teeth with numerous lateral denticles and prominent central cusp. Reproductive system androdialucic with semiserial receptaculum seminis. Bursa copulatrix absent. Penis with posteriorly directed, subterminal spine.

Type species: *Anetarca armata* Gosliner, sp. nov.

Etymology: *Anetarca* is derived from the reversal of the letters forming the genus *Cratena* Bergh, 1864, to which the new genus appears to be allied. The letter "a" was added to the end of the name for euphony. BURN (1969) described *Sclerodoris tarka* based on the Australian aboriginal word *tark*, for a spear. In the present genus, the *tarc* portion of the name also refers to apical penial spine.

Anetarca armata Gosliner, sp. nov.

(Figures 1D, 9–11)

Type material: Holotype, California Academy of Sciences, San Francisco, CASIZ 074067, intertidal zone, S of Punta Asuncion, Baja California Sur, 2 July 1984, Robert Van Syoc. Paratype, CASIZ 074584, same date and locality as holotype. Paratype, dissected, CASIZ 074585, same date and locality as holotype.

Distribution: This species is known only from the type locality along the northern Pacific coast of Baja California Sur.

Etymology: The specific epithet, *armata*, refers to the presence of a posteriorly directed penial spine, which distinguishes this species.

External morphology: The living animals (Figures 1D, 9A) reach 14 mm in length. The general body color is translucent reddish orange. Almost the entire body surface is mottled by patches of opaque cream-white. The size and density of the patches are extremely variable within a single individual. The rhinophores are largely devoid of opaque patches and are a deeper orange than the rest of

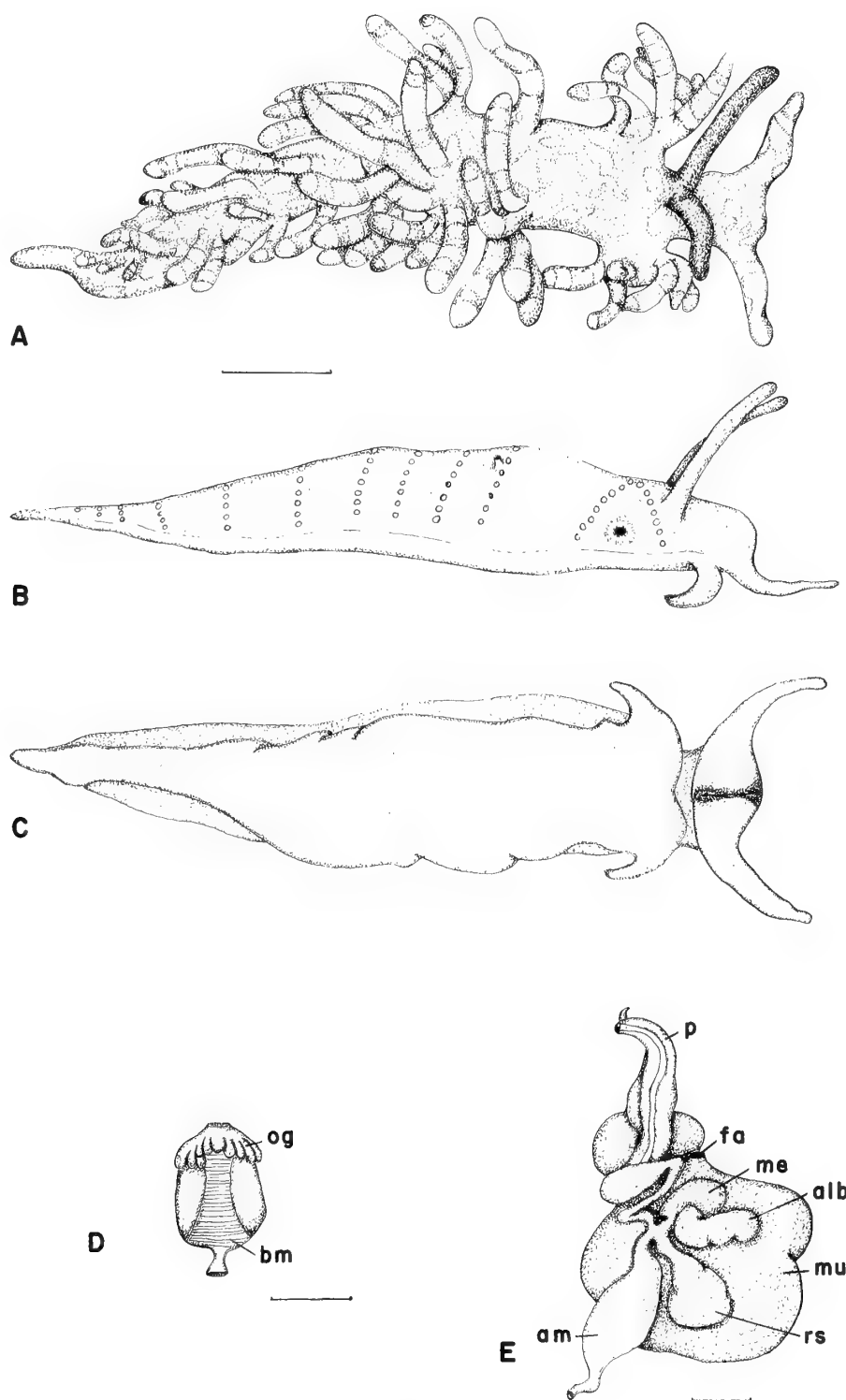


Figure 9

Anetarca armata gen. et sp. nov. A. Dorsal view of living animal: scale = 2 mm. B. Lateral view of preserved animal showing arrangement of cerata: scale = 2 mm. C. Ventral view of head and foot: scale = 2 mm. D. Buccal mass: bm, buccal mass; og, oral gland; scale = 0.5 mm. E. Reproductive system: alb, albumen gland; am, ampulla; fa, female aperture; me, membrane gland; mu, mucous gland; p, penis; rs, receptaculum seminis; scale = 0.5 mm.

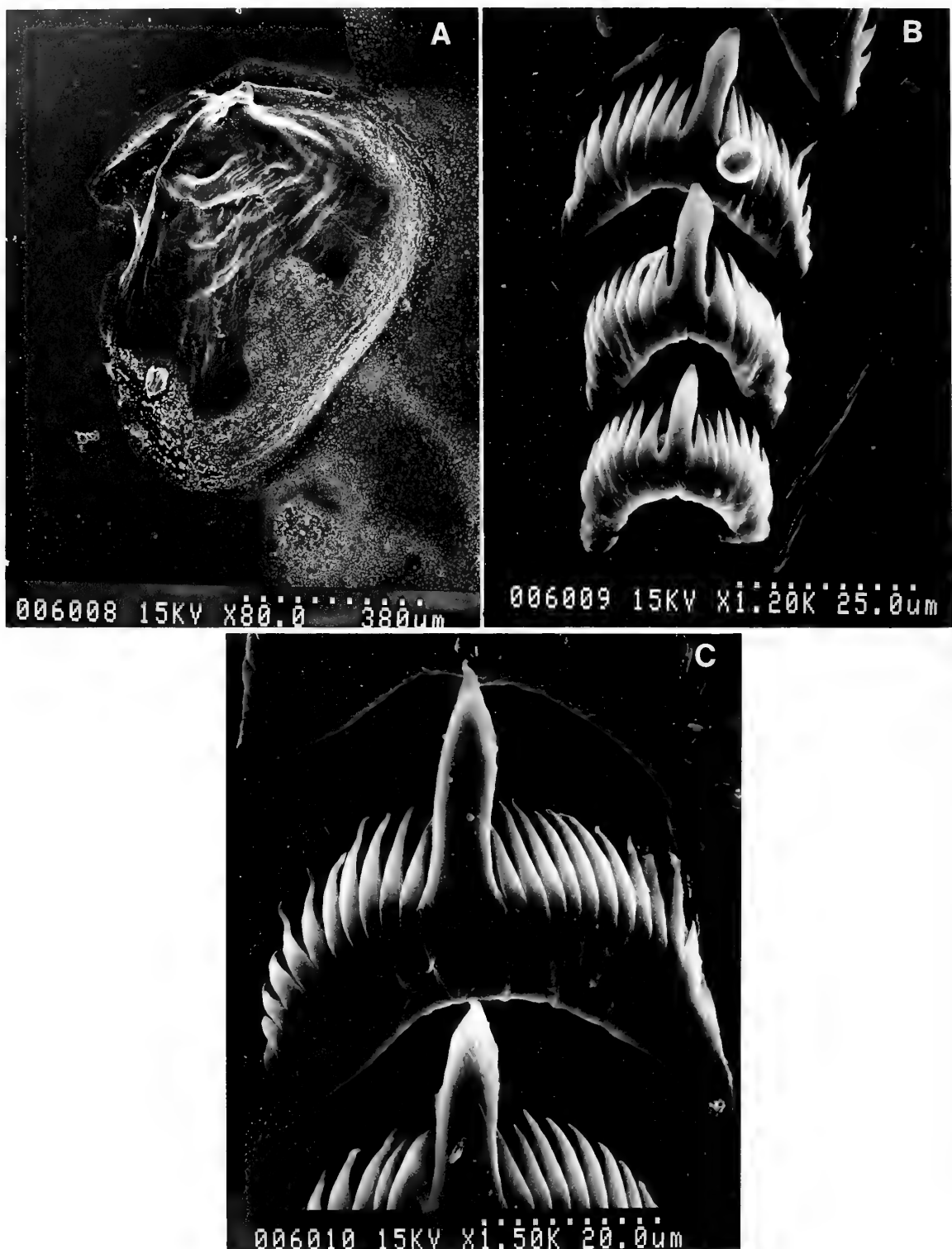


Figure 10

Anetarca armata gen. et sp. nov. Scanning electron micrographs. A. Jaw. B. Older radular teeth. C. Newer radular teeth.

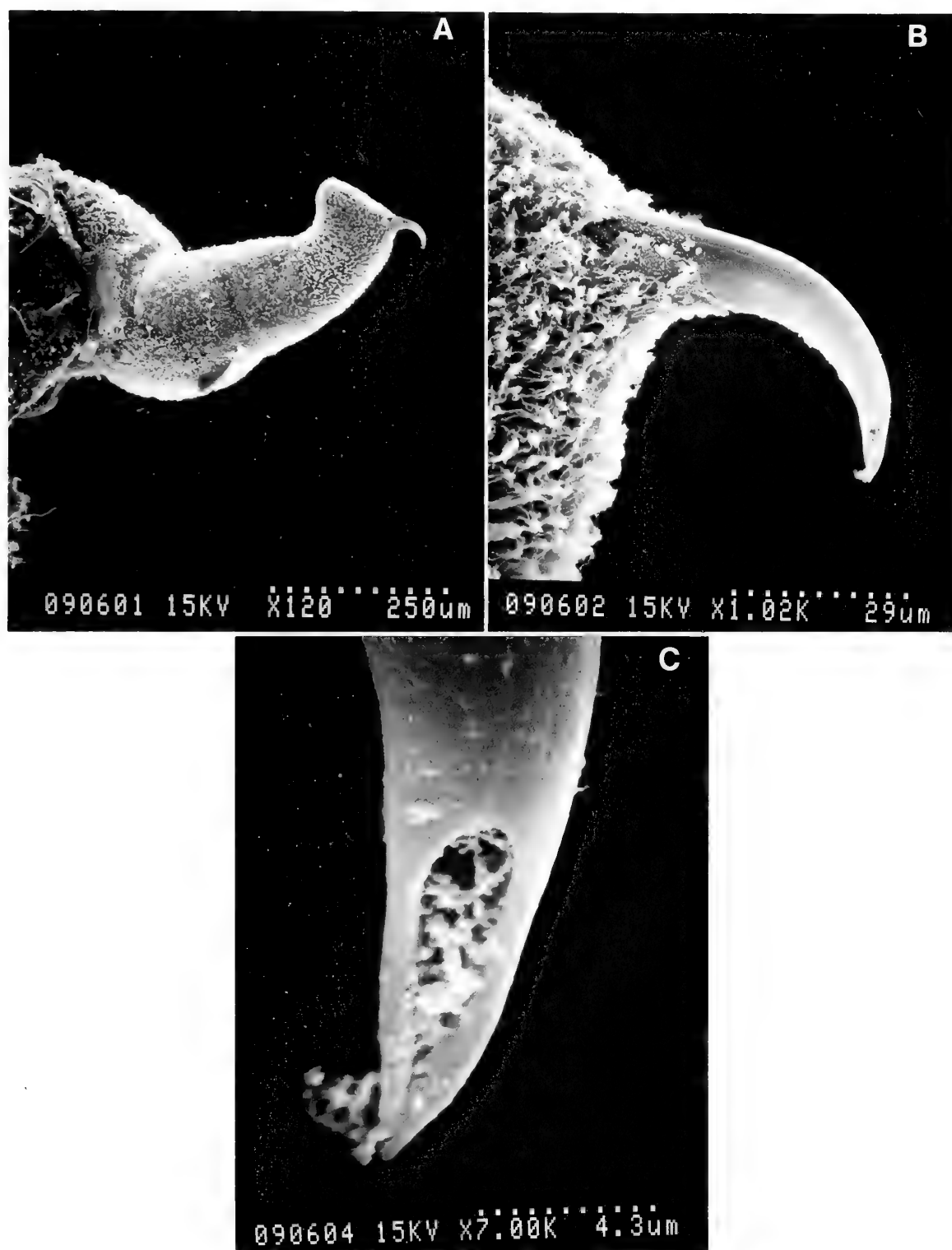


Figure 11

Anetarca armata gen. et sp. nov. Scanning electron micrographs. A. Penis. B. Penial spine. C. Apex of penial spine.

the body. Opaque pigment is present on the head, the oral tentacles, and as irregular transverse bands on the cerata.

The head, foot, and notum are broad, giving the animal a robust appearance. The smooth and elongate rhinophores are broadest basally and taper to a narrow apex. The oral tentacles are shorter than the rhinophores and are relatively stout. The foot corners (Figure 9B) are elongate and tentacular. The ventral portion of the head is deeply cleft and bilabiate (Figure 9C). The cerata are curved and are cylindrical throughout most of their length, but taper to an acute apex. The precardiac cerata are arranged in a single horseshoe-shaped arch that contains only a single row of cerata (Figure 9B). The postcardiac cerata are arranged in a series of 9 or 10 linear rows. The ceratal formula in one specimen is: I-15, II-7; III-7, IV-7, V-7, VI-6, VII-5, VIII-4, IX-3, X-2, XI-1. The gonopore is situated within the arch of the precardiac cerata. The anus is cleioproctic, situated posterior to the first postcardiac ceratal row. The nephroproct is situated within the inter-hepatic space.

Buccal mass: The buccal mass is short and muscular. A series of lobed oral glands is present on the dorsal surface of the buccal mass (Figure 9D). The jaws (Figure 10A) are broad with a moderately long masticatory border. The border is smooth, without any evidence of denticulation. The radular formula is $13 \times 0.1.0.$ in one specimen examined. The teeth are narrow and broadly arched. The central cusp is broad and elongate. On either side of the cusp are numerous elongate denticles. Older teeth (Figure 10B) may have as few as 8 denticles on either side of the cusp, while newer ones (Figure 10C) may have as many as 11 denticles.

Reproductive system: The arrangement of organs is androdiaulic (Figure 9E). The narrow preampullary duct expands into a curved, saccate ampulla that narrows and divides into a short oviduct and a narrower vas deferens. The oviduct is joined by the thick duct of the semiserial, pyriform receptaculum seminis. Slightly distal to this junction the oviduct enters the female gland mass between the albumen and membrane glands. These two glands are small compared to the lobate mucous gland. The mucous gland terminates at the female gonopore. The vas deferens is narrow proximally and expands into the large penis. There does not appear to be a distinct prostatic region of the vas deferens. The penis curves and enters the penial sac. Within its central portion the narrow penial duct is visible. The penial papilla is curved at its distal apex. At this point the penial duct emerges from the papilla. Near the distal end of the papilla, a chitinous spine is visible (Figure 11A). The spine is sharply curved away from the tip of the penial papilla (Figure 11B). The tip of the penial stylet bears an elongate opening at its apex (Figure 11C), which appears similar to the tip of a hypodermic needle. How the stylet functions is uncertain because it does not appear to be in direct contact with the penial duct.

Discussion: The systematic relationships of the Facelinidae have been reviewed and discussed extensively in recent years (MILLER, 1974; GOSLINER, 1980; EDMUNDS & JUST, 1983; GOSLINER & BEHRENS, 1986; WILLAN, 1987). The family has been divided into subfamilies, largely on the basis of differences in ceratal arrangement (ER. MARCUS, 1958; MILLER, 1974). EDMUNDS (1970) suggested that ceratal arrangement has evolved in a polyphyletic fashion within the family, and GOSLINER (1980) has supported this view.

Since then, RUDMAN (1981) studied the clearly monophyletic facelinid genus *Phyllodesmium*. In this genus, monophyly is highly probable, given the several synapomorphies that unite the species, including absence of cnidosacs, flattened cerata that readily autotomize, and a specialized diet of alcyonarians. RUDMAN (1981: fig. 27) depicted the ceratal arrangement in the various species he studied. The genus *Phyllodesmium* includes species that have cerata contained in arches with one or more rows of cerata within the arches. There are also several species that have only a preanal arch, followed by postanal linear rows, as in the genus *Cratena* Bergh, 1864. Because members of this single genus exhibit most of the ceratal patterns known for members of the family, there remains no question that the ceratal patterns have evolved polyphyletically.

I agree with WILLAN's (1987) hypothesis that, within the Facelinidae, having all cerata arranged in linear rows represents the plesiomorphic state, and that having cerata arranged in arches represents a derivation from the primitive condition. Whether or not evolution of arches from rows occurred only once in the family remains unresolved. Clearly, arches have arisen from rows on at least one other occasion in the Aeolidiidae (GOSLINER, 1985). I would also suggest that, for species of facelinids with arches, those arches with more than one row of cerata are plesiomorphic and those with a single row of cerata are apomorphic. This is consistent with the general trend within aeolids to reduce ceratal numbers. Also apparent in the Facelinidae has been a reduction of postanal ceratal arches to form secondarily derived linear rows, as has occurred independently in some species of *Phyllodesmium* and in *Cratena*. These secondarily derived rows differ from the plesiomorphic arrangement in that single rows are well separated from each other rather than forming clusters of dense rows.

This ceratal arrangement, with a preanal arch and single postanal rows, is also found in *Anetarca*. *Anetarca* lacks all of the above-mentioned synapomorphies present in species of *Phyllodesmium*. Species of *Cratena* are elongate, slender aeolids, whereas *Anetarca armata* is stockier. All described species of *Cratena* have a large penial gland and lack a penial stylet. No penial gland is present in *A. armata*.

Several other genera of facelinids possess a single penial stylet (MILLER, 1974). In *Emarcusia* Roller, 1972, most species of *Noumeaella* Risbec, 1937, and one species of *Favorinus* Gray, 1850, the penis bears a straight, hollow

penial stylet. The penis of *Emarcusia* also bears an accessory appendage. In species of *Phidiana* Gray, 1850, *Godiva* Macnae, 1954, and all but two species of *Herviella* Baba, 1949 (BURN, 1967; RUDMAN, 1980), there is a curved hook at the apex of the penis. *Phidiana* s.s. contains species with numerous ceratal rows per cluster, rounded foot corners, and the anus situated in the posterior half of the body. *Godiva* contains species with all cerata arranged in arches, with more than one row of cerata per arch. *Herviella* contains species with oblique rows of cerata that represent the retention of the anterior limb of a ceratal arch (Miller, 1974). Species in this genus also have rounded foot corners. In all these taxa, the penial hook is situated at the end of the efferent duct. The spine curves inwardly, toward the penial apex. In contrast, the penial hook found in *Anetarca* is subterminal and curves in the opposite direction. On the basis of its unique structure, I hypothesize that the penial hook of *Anetarca* has evolved independently from other chitinous hooks found in other facelinids. On this basis, *Anetarca* cannot be readily accommodated into any existing genus and is considered to be distinct from all other described facelinids.

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Morphological Variability in the Gastroesophageal Ganglion of the Nudibranch *Tritonia diomedea*

by

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Abstract. Gastroesophageal ganglia are occasionally missing from their normal location in the nudibranch *Tritonia diomedea*. When the identifiable gastroesophageal ganglion neuron G1 is absent from the gastroesophageal ganglion, it is found in the buccal ganglion. The rate of occurrence of this anomaly, which ranged from 3 to 20%, is dependent on animal collection site. Genetic differences and environmental effects are considered as possible reasons for between-site variability in this anomaly. These results suggest that gastroesophageal ganglion neurons may be present in other non-nudibranch opisthobranchs, but because of differences in timing of neuron development and in neuron migration, they develop in the buccal ganglion.

INTRODUCTION

The gastroesophageal ganglion (*geg*) is a morphological character that distinguishes nudibranchs from other opisthobranch mollusks (RUSSELL, 1929). This small ganglion, attached to the lateral margin of the buccal ganglion, is classed by BULLOCK & HORRIDGE (1965) with evolutionarily labile accessory ganglia. The *geg* typically has a number of small neurons and a giant neuron, G1, with its axon extending in a nerve along the esophagus to the stomach. The neuron G1 has been studied electrophysiologically in *Anisodoris nobilis* (MacFarland, 1906) by GORMAN & MIOLLI (1969), and a similar neuron has been identified with antibodies in *Tritonia diomedea* (Bergh, 1894) and other nudibranchs (LONGLEY & LONGLEY, 1985; MASINOVSKY *et al.*, 1988).

In specimens from the same species, the configuration of the gastroesophageal ganglion and the identifiable neuron G1 may vary. In the nudibranch *Archidoris pseudoargus* (Rapp, 1827), ROSE (1971) found that the left gastroesophageal ganglion and G1 were fused with the left buccal ganglia about 5% of the time. I report here a generally similar anomaly that may occur in either the left or right gastroesophageal ganglion in *Tritonia diomedea*.

MATERIALS AND METHODS

The Pacific coast nudibranch used in this study has been identified as *Tritonia diomedea* by THOMPSON (1971) and was obtained locally by trawling at three sites in Puget

Sound (Figure 1). *Tritonia diomedea* collected in Bellingham Bay (KEMPF & WILLOWS, 1977) apparently feed on *Virgularia* sp.; however, animals collected in East Sound by WILLOWS (1967) were found with *Stylatula elongata* (Gabb, 1863). *Tritonia diomedea* obtained from Santa Monica Bay, California, were collected in the vicinity of the Hyperion outfall system by Pacific Biomarine Supply Co., Los Angeles, California, and are also typically found with *Stylatula elongata* (personal communication from Marion Patton). Animal weight ranged from 5 to 400 g.

Collection years at each site and numbers of animals used in determining the frequency of G1 in the buccal ganglion are given in Table 1. For East Sound and Bellingham Bay sites, several trips were made to each site during a year and a number of trawls were made in the general area of the site each trip. In the latter part of the 1970s when trips to East Sound were generally unsuccessful, efforts to restock this site were made by depositing in East Sound egg strings and small animals collected in Bellingham Bay (personal communication from David King, captain of the collection vessel *Hyda*). Animals from Port Townsend were collected in one trawl, and animals from Santa Monica Bay were received in a single shipment.

The location of G1, which was visually identifiable because of its large size and orange pigmentation, was determined with a dissecting microscope. In addition, in some preparations one of the following histological procedures was used to identify the location of G1 and to show the number of neurons and neuron size relations in the gastroesophageal and buccal ganglia. (1) Ganglia were stained in 0.01% methylene blue seawater to enhance visibility of neurons. (2) Nerves were backfilled with cobalt chloride

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Figure 1

Map of northern Puget Sound indicating collection sites: East Sound (1), Port Townsend (2), and Bellingham Bay (3).

by placing ganglia in seawater and isolating with a petroleum jelly dam the freshly cut nerve in 3% CoCl_2 . After 24 hr at 4°C, these ganglia were washed in seawater, treated with 1% ammonium sulfide solution in seawater to precipitate the CoCl_2 , fixed in Carnoy's, dehydrated in ethanol, and cleared and photographed in methyl salicylate. (3) Buccal and gastroesophageal ganglion paraffin sections were stained using the Feulgen reaction (STOWELL, 1945).

RESULTS

In *Tritonia diomedea* the gastroesophageal ganglion (*geg*), which is attached through a short connective to the anterolateral edge of each buccal ganglion (Figure 2), is variable in size and may be reduced in cell number or missing entirely from its usual location (Figure 2A, B). The anterior location of this ganglion relative to the buccal ganglion (*bg*) in *T. diomedea* results from the rotated position of the buccal mass such that the buccal ganglia lie on its dorsal surface under the esophagus rather than in a more typical position under the buccal mass.

When the *geg* is attenuated in size or is absent, nerves that normally arise from the *geg* still branch from its short

Table 1

Collection site, year, and number of animals from each site.

Collection site	Number of animals collected at each site				
	1977	1978	1981	1988	1989
Bellingham Bay	43	15	—	28	19
Santa Monica Bay	—	—	—	28	—
Port Townsend	—	37	—	—	—
East Sound	5	2	52	—	—

connective near the buccal ganglion, but it has not been determined how numbers of axons in these nerves vary with the size of the *geg*. Cobalt backfills of *geg* nerves show that some axons in these nerves come from peripheral somata and enter the buccal ganglion or come from somata in the buccal ganglion. In salivary duct nerves, which enter the *bg* through the *geg* connective, axons arise from peripheral neurons, enter the buccal ganglion, pass through the buccal commissure, and exit the ganglia through the contralateral homologue of the nerve from which they originated.

Other than the identifiable neuron G1 (Figure 2), specific *geg* neurons with axons in *geg* nerves have not been identified. The most medial of these nerves, the gastroesophageal nerve (*gen*), carries the axon of G1, and in the absence of the *geg*, this nerve appears to be the principal continuation of the *geg* connective. Individual neurons smaller than G1, and occasionally a neuron identified as G1 on the basis of its size and pigmentation, may be attached to the *gen* adjacent to but distal to the *geg*, i.e., the *geg* is not always well-defined. When G1 could not be identified in the *geg* or on the *gen*, a neuron similar to G1 in size and pigmentation was found in the buccal ganglion near the axon tract that forms the *geg* connective (except in 3 of 458 ganglia in which G1 could not be located).

In Figure 2B, cobalt backfills of the left and right gastroesophageal nerves show a typical result when one G1 is in the buccal ganglion and its contralateral homologue is in its normal location in the *geg*. Following the nomenclature of MASINOVSKY *et al.* (1985), the two anterodorsal buccal ganglion neurons of intermediate size that also have axons in the *gen* and are shown by cobalt backfills of the *gen* (Figure 2B) are identified as B11 and B12. In the anterior part of the *bg*, most of the neurons are small with only a few neurons of intermediate size, such that when G1 is anomalously located there, on the dorsal surface or anterior edge of the buccal ganglion, it is easily recognized by its size and pigmentation. This is shown in Figure 2C, where the size of the G1 nucleus can be compared to those of the smaller neurons in the *geg* and the anterior part of the buccal ganglion near the *geg* connective.

Examples of the gastroesophageal ganglion neuron G1 appearing in the buccal ganglion in *Tritonia diomedea* were

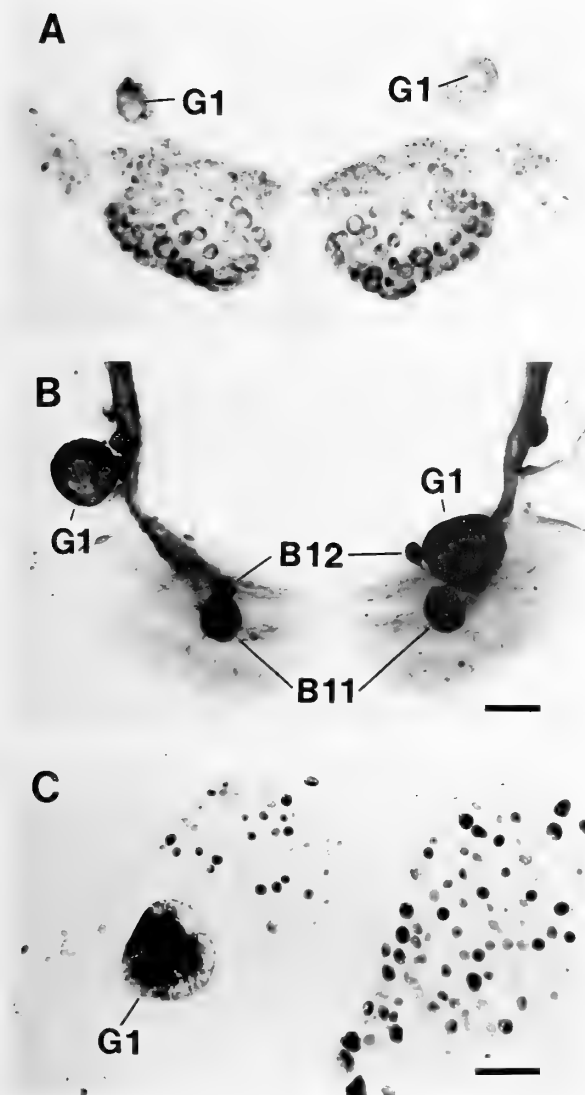


Figure 2

A. Methylene blue stained buccal and gastroesophageal ganglia showing distribution of neuron sizes and normal location of G1 neurons in the gastroesophageal ganglia. B. Cobalt chloride back-filled gastroesophageal nerves showing G1 in the gastroesophageal ganglion (*geg*) on the left and in the buccal ganglion on the right. Bilaterally symmetric B11 and B12 neurons, which also have axons in the gastroesophageal nerves, are indicated. C. Feulgen stained nucleus of G1 in the *geg* and nuclei of smaller neurons in the *geg* and anterior part of the buccal ganglion (10 μ m paraffin section). Size bar in B (for both A and B) = 250 μ m. Size bar in C = 50 μ m.

found in animals from all collection sites. The number of animals from each collection site and the number of anomalies (G1 in *bg*) in the left and right ganglia are given in Table 2. Although the frequency appears higher for the left buccal ganglion, the difference between the estimated probability of G1 in the *bg* on the left ($P = 0.157$) and on

Table 2

Number of G1 neurons found in buccal ganglia (*bg*) and the probability of G1 occurring in the *bg* for each collection site.

Collection site	Number of animals	Left <i>bg</i> anomalies	Right <i>bg</i> anomalies	Probability
Bellingham Bay	105	24	17	0.195
Santa Monica Bay	28	6	2	0.143
Port Townsend	37	3	6	0.122
East Sound	59	3	1	0.034
Totals	229	36	26	0.135

the right ($P = 0.114$) is not significant ($z = 1.44$, $0.1 > P > 0.05$, one-tailed test). In four animals from Bellingham Bay and in one animal from Santa Monica Bay, both gastroesophageal ganglia were missing and the G1 neurons were found in both left and right buccal ganglia, as would occasionally be expected if this anomaly occurred randomly and independently in left and right ganglia. In the absence of a significant left-right bias, data from left and right ganglia are grouped together in comparing the probability of G1 in the *bg* at different times and from different collection sites. For animals collected from Bellingham Bay over a period of years, the estimated probability of G1 in the *bg* in 1977 ($P = 0.22$), 1978 ($P = 0.20$), 1988 ($P = 0.18$), and 1989 ($P = 0.16$) does not seem to have changed significantly, although it may be slowly declining. Estimated probabilities of G1 in the *bg* for each collection site are shown in Table 2. When animals from Bellingham Bay, Port Townsend, and Santa Monica Bay are compared using the Chi-squared test, the hypothesis that these probabilities are equal cannot be rejected ($\chi^2 = 2.04$, $0.25 > P > 0.1$, d.f. = 1). However, the hypothesis of equal probability of this anomaly at different sites is solidly rejected when East Sound is included as a fourth site ($\chi^2 = 14.7$, $P < 0.001$, d.f. = 2).

DISCUSSION

Morphological observations suggest that the neuron identified as G1 in the buccal ganglion (*bg*) is the same as the G1 neuron normally found in the gastroesophageal ganglion (*geg*). G1 in the *geg* is similar in size and pigmentation to its putative counterpart found in the *bg*. The axon of this neuron in the buccal ganglion follows the same path into the gastroesophageal nerve as G1 in the *geg*, and the neuron presumed to be G1 is found in the *bg* only when G1 is absent from the *geg*.

Unlike in *Archidoris pseudoargus*, where G1 was found predominantly in the left buccal ganglion (ROSE, 1971), in *Tritonia diomedea* there does not appear to be a clear left-right bias for this anomaly. The anatomical differences observed in the *T. diomedea* gastroesophageal ganglion are

not readily described as simply a partial fusion or fusion of this ganglion with the buccal ganglion, as reported for *A. pseudoargus* by ROSE (1971). In all cases in *T. diomedea* when the *geg* was missing, its nerves did not arise individually from the buccal ganglion but rather from the *geg* connective, which was always present; *i.e.*, the normal site of development of the *geg* was retained. Smaller neurons that appear to be missing from the *geg* may develop in the buccal ganglion as G1 apparently does, or alternatively, some or all of these neurons may simply fail to develop.

In animals from Bellingham Bay collected in four different years over a 13 year period, the variability observed in the development of the *geg* was consistently high, which suggests that the factors that produced this variability were present throughout this period. Consistent with this result, single samples from the Port Townsend and Santa Monica Bay sites also show high variability of G1 position. Statistically significant data from East Sound showing low variability in the position of G1 are available for only one summer. In the absence of other information, these results might suggest that high variability is normal and that low variability in *geg* development is the novel condition. However, because the gastroesophageal ganglion has been historically described as a normal characteristic of nudibranchs (BULLOCK & HORRIDGE, 1965; RUSSELL, 1929), animals collected in East Sound, where variability in the *geg* was low, are considered here to be examples of a more normal development of the nervous system in comparison to animals collected at other sites where *geg* variability was high.

The finding of a significantly lower rate for G1 in the buccal ganglion in animals from East Sound, when compared to animals from the other three sites, could be caused by genetic and/or environmental differences. The extent of genetic isolation of veligers settling to metamorphose at the different sites depends on the dispersal of the veligers in the planktonic phase, which lasts at least five weeks in *Tritonia diomedea* (KEMPF & WILLOWS, 1977). It is likely that animals from Santa Monica Bay, which is exposed to an open-ocean environment, are not genetically isolated from other *T. diomedea* along the California coast because of wide dispersal during such a long planktotrophic period (STRATHMANN, 1974), but the long distance between Santa Monica Bay and Puget Sound (2000 km) could produce genetic isolation between animals from these two areas. In Puget Sound the greatest difference in variability in development of the *geg* was between animals from the Bellingham Bay and East Sound collection sites, which are about 30 km apart (Figure 1). In Bellingham Bay the typical residence time of seawater is 4–5 days with a range of 1–11 days (BECKER *et al.*, 1989), while from a study of sand dollar larvae in East Sound (EMLET, 1986), the residence time of larvae in East Sound appears to be less than two weeks. The apparent exchange of external seawater into these sites and the vertical mixing of this seawater by tidal action (WALDICHUK, 1957) as in Rosario Strait, which

separates these sites and has tidal currents of 10 km/hr with runs up to 30 km (THOMSON, 1981), suggest that *T. diomedea* in the Bellingham Bay and East Sound sites come from a common planktotrophic population of veligers and are not genetically isolated. This does not rule out the possibility of genetic differences in adults from these sites, however, because strong selection by different environments at these sites can result in genetic differences in the animals that mature (SLATKIN, 1985).

The low salinity of surface water in Bellingham Bay, which occurs seasonally near the Nooksack River delta, may be an environmental factor that could affect early development of veligers before they settle to metamorphose (if they are present in this surface layer). Studies of development in the nudibranch veligers of *Doridella steinbergae* (BICKELL & CHIA, 1979), *Melibe leonina* (BICKELL & KEMPF, 1983), and *Tritonia diomedea* (KEMPF *et al.*, 1987) have shown that the buccal ganglion, and presumably the attached gastroesophageal ganglion, does not appear until the veliger is on the substratum just prior to metamorphosis. This timing suggests that factors affecting the variability in the location of G1 are associated with development while the animals are on or near the substratum rather than while they are in the low-salinity surface water. The absence of low-salinity surface water comparable to that in Bellingham Bay at the Port Townsend and Santa Monica Bay sites, where variability in the position of G1 is also high, suggests that low-salinity surface water is not a cause of this variability.

Other environmental factors during early development in the veliger phase such as temperature and food would not be different for animals in the East Sound and Bellingham Bay sites because of the intermixing of seawater in this area. Veligers in Santa Monica Bay may be exposed to a warmer temperature and develop faster than those in Bellingham Bay, but the variability in the location of G1 is not statistically different at these two sites, which suggests that temperature is not an environmental factor that produces this developmental variability. In the laboratory, *Tritonia diomedea* will feed on a variety of octocorals, but the normal diet of this species is not well documented (WILLOWS, 1978). The metamorphosing animal will feed on *Virgularia* sp. (KEMPF & WILLOWS, 1977), which is apparently present in Bellingham Bay, but *Stylatula* has been reported with *T. diomedea* in East Sound and Santa Monica Bay, and in the laboratory *T. diomedea* prefers *Stylatula elongata* over *Virgularia* sp. (WILLOWS, 1978). Thus, there is no clear correlation with the type of food available to the newly metamorphosed animal and the amount of variability in the development of the *geg*.

Teratogenic substances in bottom sediment may contribute to variability in the development of the *geg* if neurons are migrating to this ganglion after the veliger has settled to the substratum. Supporting this possibility is the fact that pollution from industry or municipal wastewater has been reported at each of the three collection sites that

have high rates of G1 in the buccal ganglion (MPERA, 1971; SCCWRP, 1973; PSEA, 1987). For East Sound in the San Juan Islands, which have no heavy industry and are considered environmentally clean, pollution in bottom sediments is presumed to be relatively low, although no measurements from this area have been reported. This sparsity or absence of data is a ubiquitous problem in trying to assess the effects of pollution at different sites. Dioxins and furans, which have caused fishing bans and consumption advisories at coastal sites around pulp paper mills along Georgia Strait (personal communication from M. Nassichuk, Fisheries and Oceans, Vancouver, B.C.), may also have accumulated from pulp paper mill or municipal wastewater discharges at the Bellingham Bay, Port Townsend, and Santa Monica Bay sites; however, no measurements of these teratogenic chemicals have been reported for bottom sediments or biological samples at these sites. Mercury, one teratogenic chemical that has been reported at these sites, has been correlated with abnormal neuron migration (CHOI *et al.*, 1978), has been shown to have teratogenic effects at concentrations lower than those reported in collection site sediments (DIAL, 1978; SCHOWING & BOVERIO, 1979), and has been found to accumulate in the food chain, *e.g.*, in spiny dogfish around the Fraser River delta in Vancouver, British Columbia, (FORRESTER *et al.*, 1972). This correlation of abnormal development of the gastroesophageal ganglion in *Tritonia diomedea* with the presence of teratogenic chemicals in bottom sediments suggests that such chemicals may act on the developing nervous system and affect the location of G1 and other *geg* neurons. If this is the case, small changes in the nervous system, such as the anomaly described here, may be a sensitive indicator of environmental pollution.

The bilateral symmetry of the *geg* may provide sufficient redundancy such that only one ganglion is necessary in a viable animal. In five instances, however, *Tritonia diomedea* were found with G1 neurons in the buccal ganglia and both gastroesophageal ganglia missing. The fact that *T. diomedea* is viable without a *geg* suggests that the location of neurons in the *geg* is not a necessary anatomical feature in nudibranchs, but is present in nudibranchs and not in other opisthobranchs because of small developmental timing differences in the central nervous system and differences in neuron migration. Such differences may affect gross morphology of the nervous system and neuron location without affecting essential characteristics of individual neurons. This possibility also implies that a neuron functionally similar to G1 may be present in the buccal ganglia of other gastropod species that are closely related to nudibranchs but that do not normally have a gastroesophageal ganglion.

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Female Genital System of *Chorus giganteus* (Prosobranchia: Muricidae)

by

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Abstract. The female genital system of *Chorus giganteus* has evolved and specialized in accordance with the requirements of internal fertilization. It includes the renal and pallial oviducts. The pallial oviduct is composed of a glandular region, which is differentiated into albumin and capsule glands, and a nonglandular region formed by the seminal receptacle, the bursa copulatrix, and the genital pore. The epithelium of the seminal receptacle of *Chorus giganteus* is of the simple glandular type, and many secretion granules are gathered at the surface, suggesting a possible nutritive function.

INTRODUCTION

The muricids are considered to be some of the most advanced of the prosobranchs. All exhibit internal fertilization and have complex behavior patterns. A highly specialized reproductive system permits the animal to deposit many eggs within an individual capsule.

Many neogastropods do not have a free-living larval stage. In some species with direct development, all the young emerge as miniature adults. In other species, however, many eggs are deposited within each of several capsules, but only a few develop; the remainder, termed nutritive eggs, serve as a food source for the developing embryos (THORSON, 1935, 1940; RADWIN & CHAMBERLAIN, 1973; MOORE & SANDERS, 1978; GALLARDO, 1980).

The female genital system of neogastropods has evolved and specialized in accordance with the requirements of internal fertilization and the deposition of eggs within a capsule (FRETTER, 1941, 1946, 1953). The system includes a glandular region for supplying nutritive and capsule-forming materials, the latter being secreted around the eggs after fertilization. The pallial oviduct has been modified for the development of accessory structures such as the seminal receptacle, the bursa copulatrix, and the ingesting gland, in which the autolysis of superfluous sperm takes place. These structures are common throughout the order Neogastropoda, although there are differences between species in their location and the presence or absence of particular structures. The objective of this paper is to describe the reproductive system of the muricid *Chorus giganteus*, and to compare it with that of some other neogastropods.

MATERIALS AND METHODS

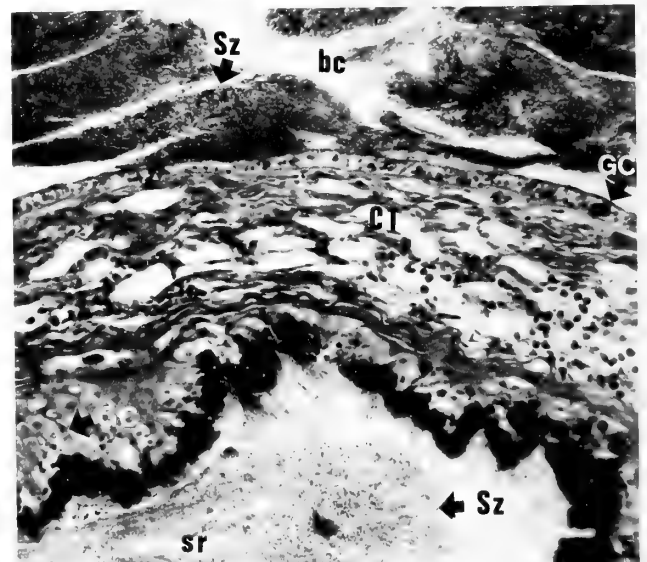
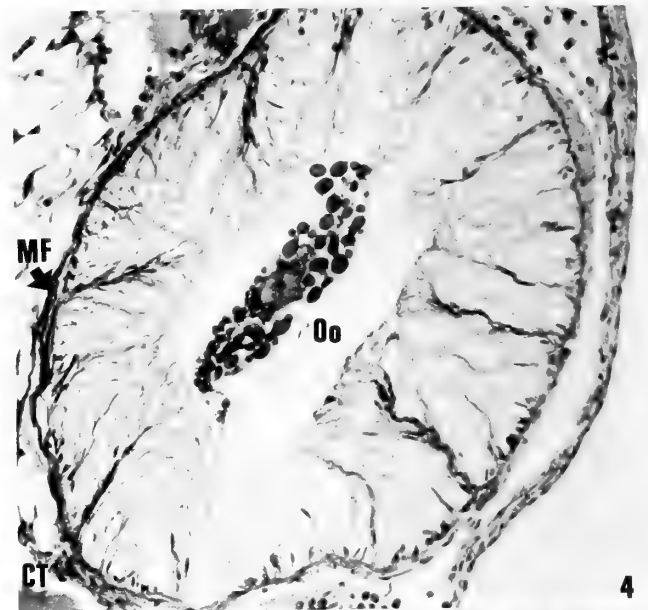
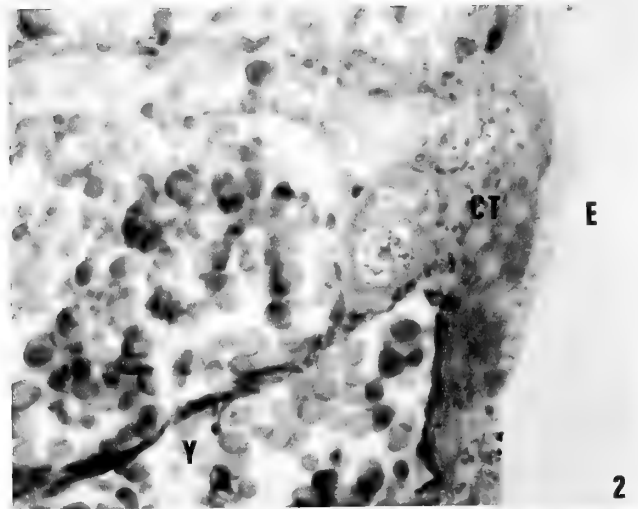
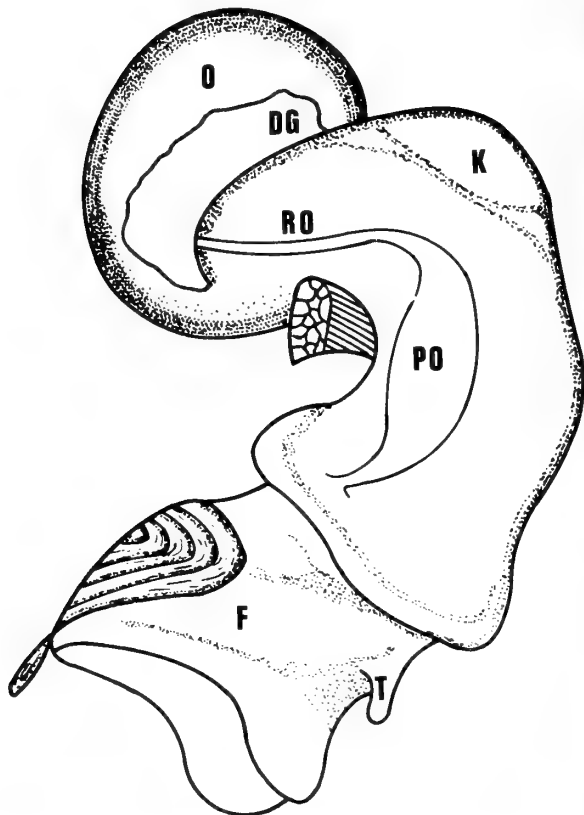
A total of 10 male and 10 female specimens of *Chorus giganteus* were collected by s.c. at Puerto Claro, Valdivia (39°53'S, 73°22'W). Five male and five female individuals were dissected, and the whole male gonad or the female gonad plus the pallial oviduct was fixed with Hollande Bouin (picric acid-formalin-acetic acid plus copper (II) acetate mixture) for 24 hr. Embedded tissue was sectioned at 5–10 μ m and placed serially on slides. Tissue was dehydrated in a series of increasing ethanol solutions, and sections were stained with azocarmine and hematoxylin-eosin.

In addition to the specimens dissected for gonads, macroscopic dissections were made of five males and five females under a Leitz Wetzlar stereomicroscope.

RESULTS

Chorus giganteus is a gonochoristic species that has no apparent external sexual dimorphism. The gonad and visceral mass (Figure 1) are surrounded by the pallial epithelium, which is a single layer of cuboidal cells having clear, homogenous cytoplasm and spherical, centrally located nuclei. Beneath the epithelium lies a thin layer of dense connective tissue containing muscle fibers. This connective tissue, which is less densely packed in the deeper part of the gonad, is arranged in irregular segments, and supports the ovarian tubules (Figure 2).

The ovary is yellow to dark brown in color, depending on the stage of maturation. It is located in the most distal part of the visceral mass, in the ultimate and penultimate



(part) whorls of the shell, and lies adjacent to the digestive gland (Figure 1). The ovary is a multilobed organ containing large tubules oriented perpendicularly to the spiral axis. The ovarian tubules, some of which intrude between the diverticula of the digestive gland, are separated from one another by a sheet of loose connective tissue projecting perpendicularly from the gonad wall or the mantle. Under this sheet, from which it is separated by the basal lamina, is located the germinal epithelium. Follicle cells and young oocytes lie closest to the basal lamina (Figure 2), whereas vitellogenic and postvitellogenic oocytes occur near the center of the tubule.

The ovarian tubules join to form a single oviduct, which emerges from the ovary and extends along the columellar side of the visceral mass, beneath the pallial epithelium. At the posterior limits of the mantle cavity, the oviduct abruptly enlarges. The enlarged portion continues in the mantle roof.

The oviduct consists of two morphologically distinct portions, a renal component and a pallial component (Figure 1). The former, which is more proximal to the ovary, passes along the visceral mass before enlarging to form a glandular region, the pallial oviduct, which traverses the mantle and terminates near the right tentacle. In gross histological sections, the pallial oviduct is the more visible of the two components, and varies in length from 3 to 6 cm, according to the stage of maturity of the female.

The renal oviduct (200–300 μm diameter), which lies embedded in connective tissue under the pallial epithelium, has a wall composed of a thin circular muscle and some connective tissue cells (Figure 4). It is lined with a simple columnar epithelium that lies on a thick basal lamina. These epithelial cells vary in height, giving the cell layer an irregular surface.

The pallial oviduct is composed of a glandular region, formed by the more enlarged section, and a nonglandular region (Figure 2). The former is differentiated into two regions, the albumin gland and the capsule gland (Figure 6), both of which are composed of a right and left lobe when viewed in cross section. These lobes are connected by thin walls that give the lumen of the oviduct the appearance of a dorsoventral slit (Figure 6B, C).

The albumin gland is the part of the glandular region closest to the ovary (Figure 1); and it is formed by tall

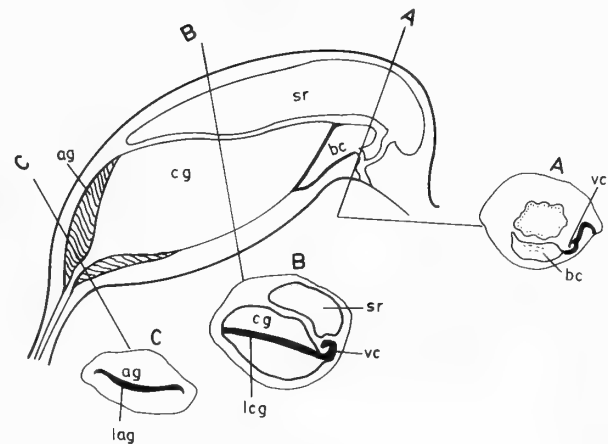


Figure 6

Line drawing (not to scale) of a longitudinal section of the pallial oviduct (right side view). A, B, and C show transverse sections. ag, albumin gland; bc, bursa copulatrix; cg, capsule gland; lag, lumen albumin gland; lcg, lumen capsule gland; sr, seminal receptacle; vc, ventral channel.

columnar epithelial cells that have a basal cell nucleus. Crypts are produced in the wall of the gland by invagination of the epithelium, and beneath these crypts lies a compact mass of glandular acini that release secretions into the lumen.

The capsule gland is more distal to the ovary (Figures 1, 6). Its lumen is lined with small cuneiform cells that overlie clusters of pyriform glandular cells with spherical, basal nuclei. These glandular cells are elongate, and their cytoplasm contains secretory granules that are released into the lumen after migrating through the elongated neck of the cell. These necks are extended toward the surface and the tips reach the lumen, where they are interspersed with cuneiform ciliated cells.

The capsule gland stains differentially with hematoxylin and eosin—the lobes appear light red and the connecting walls pale violet—or with azocarmine—in which these structures stain dark red and pale blue/violet, respectively.

The nonglandular region is formed by the seminal receptacle, bursa copulatrix, and the genital pore (Figure 6A–C).

Explanation of Figures 1 to 5

Figure 1. Female *Chorus giganteus*, whole animal, shell removed. DG, digestive gland; F, foot; K, kidney; O, ovary; PO, pallial oviduct; RO, renal oviduct; T, tentacle.

Figure 2. Cross section of ovary ($\times 400$) showing the pallial epithelium (E). CT, connective tissue; Oo, oocyte; Y, yolk.

Figure 3. Cross section of genital pore ($\times 80$). Sz, spermatozoa.

Figure 4. Cross section of renal oviduct ($\times 250$). Oo, oocyte; CT, connective tissue; MF, muscle fibers.

Figure 5. Cross section ($\times 360$) of bursa copulatrix (top) and seminal receptacle (bottom) showing spermatozoa. bc, bursa copulatrix; CT, connective tissue; GC, glandular cells; sr, seminal receptacle; Sz, spermatozoa.

Genital pore. The oviduct is connected with the external environment through the genital pore, situated near the right tentacle. This last portion of the oviduct consists of a cylindric, ciliated pseudostratified epithelium, with some intercalated mucous glandular cells. Beneath the epithelium lie the basal lamina and a layer of dense connective tissue (Figure 3).

Bursa copulatrix. The bursa copulatrix consists of an oval-shaped chamber that is connected with the seminal receptacle and, by means of a short duct, with the glandular portion of the oviduct (Figure 6A). This chamber has a simple cuboidal, ciliated epithelium in which some glandular cells contain an eosinophilic secretion. A basal lamina and muscle layer are found under this ciliated epithelium (Figure 5). The ducts that connect with the oviduct consist of a cylindric, ciliated epithelium. Under the basal lamina is situated a layer of connective tissue with muscle fibers (Figure 5). From the bursa copulatrix emerges a duct, the ventral channel, that runs along the bursa copulatrix and ventral region of the capsule gland. This channel, which is connected always with the lumen of the capsule gland (Figure 6A, B) is covered by a cylindric, ciliated epithelium. Inside the bursa copulatrix and the seminal channel, many spermatozoa can be found.

Seminal receptacle. The seminal receptacle is proximal to the bursa copulatrix chamber and is connected to it by a duct similar to that which connects the bursa copulatrix to the capsule gland. The seminal receptacle consists of an elongated chamber divided into two portions: the anterior portion, which is situated over the bursa copulatrix, and the posterior portion situated over the posterior one-third of the capsule gland. This receptacle was full of spermatozoa and stained a pale violet color. The wall of the seminal receptacle is covered by a glandular, simple epithelium (Figure 5). The cells of this epithelium are pyriform with spheric, basal nuclei, and many secretion granules are gathered at the surface of the epithelium. Some spermatozoa were observed scattered over the epithelium with the heads near the granules and the tails toward the lumen of the receptacle (Figure 5). The outer surface of the pallial oviduct is covered by a cylindric epithelium.

An ingesting gland was not observed in *Chorus giganteus*, and no region of the pallial oviduct appears to serve as a sperm ingesting area.

DISCUSSION

In neogastropods with the habits of depositing numerous eggs within a capsule and of internal fertilization, the female genital system has evolved and specialized in accordance with these behaviors (FRETTER, 1941, 1946, 1953). Fertilization must occur before nutritive and capsule-forming materials are secreted around the eggs, and it is most plausible that fertilization occurs in the lumen of the albumin gland of this species, because after albumin deposition, the fertilization of eggs may be obstructed (KOOL, 1988). However, spermatozoa are generally deposited at

the terminal end of the female duct (FRETTER, 1941, 1946; HOUSTON, 1976). Spermatozoa may be stored at the terminal end, within the bursa copulatrix, or they may be passed up the oviduct and stored within specialized regions connected to the gonoduct, such as the seminal receptacle or the ingesting gland (FRETTER, 1941, 1953; KOOL, 1988; OEHLMANN *et al.*, 1988; HOUSTON, 1976). In *Chorus giganteus*, sperm from a copulation probably are deposited in the bursa copulatrix and then transferred to the seminal receptacle, where they are stored.

The seminal receptacle, which occurs generally in neogastropods, may be divided, with one portion serving as an ingesting gland and the other to store sperm. *Chorus giganteus* has a seminal receptacle formed by a simple glandular-type epithelium as in *Colus gracilis* (HOUSTON, 1976); *Concholepas concholepas* (HUAQUIN, 1966), another Chilean muricid, also has a seminal receptacle, but *Colus stimpsoni* (WEST, 1979) and *Nucella lapillus* (OEHLMANN, 1988) lack this structure.

An ingesting gland or sperm resorbing areas have been reported for some neogastropods. For example, *Concholepas concholepas* (HUAQUIN, 1966), *Nucella lapillus* (OEHLMANN, 1988), and *Plicopurpura patula* (KOOL, 1988) have an ingesting gland. In *Chorus giganteus* an ingesting gland was not observed, nor was any region of the pallial oviduct seen to serve as a sperm ingesting area. The absence of an ingesting gland combined with the presence of a seminal receptacle in *Chorus giganteus* and *Colus gracilis* (HOUSTON, 1976) is in conflict with the suggestions of FRETTER (1941) and HOUSTON (1976) that these structures may have a common origin and may be homologous.

The seminal receptacle usually contains sperm oriented with their heads buried in the epithelium (HYMAN, 1967). In *Chorus giganteus* this epithelium is a simple glandular type and many secretion granules are accumulated on the surface of the epithelium. Spermatozoa with their heads buried in these granules may indicate a possible nutritive function of the seminal receptacle. This possibility was suggested for species of *Viviparus* by ANKEL (1925), who reported the survival of spermatozoa for five months after copulation, and by RAMORINO (1975), who reported that an isolated female of *Concholepas concholepas* produced fertilized ova four months after copulation.

Chorus giganteus has a ventral channel that connects the bursa copulatrix with the proximal portion of the albumin gland. This channel runs along the ventral region of the oviduct, and spermatozoa fertilize eggs at the posterior end of the pallial oviduct before they become surrounded by the secretory products of the albumin gland. Probably not all sperm that pass to the albumin gland are utilized in fertilization (WEST, 1979). In *Chorus giganteus*, the presence of spermatozoa in the albumin surrounding the eggs was observed, suggesting that excess spermatozoa are voided within the egg capsule. A similar description for *Colus stimpsoni* was reported by WEST (1979).

The albumin gland is constituted by columnar epithelial cells. Crypts are produced in the wall of the gland by

invaginations of the epithelium, and beneath these crypts lies a compact mass of glandular acini that release secretions into the lumen of the gland. This glandular formation differs from that in the albumin gland of *Thais lapillus* (FRETTER, 1941) and *Colus stimpsoni* (WEST, 1979). Indeed, no description similar to the arrangement in *Chorus giganteus* has been described for any other species. By contrast, the capsule gland of *Chorus giganteus* appears very similar to that of *Thais lapillus* (FRETTER, 1941) and *Colus stimpsoni* (WEST, 1979).

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Induced Spawning and Ontogeny of *Modiolus capax* Conrad (Bivalvia: Mytilidae)

by

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Abstract. The artificial spawning of *Modiolus capax* was successfully accomplished with the consecutive application of several stimuli, comprising 6 hr of air exposure, valve scraping, transfer to recirculating seawater at 27°C, increase in water temperature to 30°C over a 3-hr period, and addition of stripped gametes to the water. Mussels from Bahía de Los Angeles, Baja California, Mexico, subjected to this procedure registered the maximum percentage of spawning in July and August. Described here are the spawning mechanisms, morphology of the sexual products, and the embryonic development of *M. capax*. Lengths of selected larval stages were as follows: straight-hinge larvae, 108–160 μm ; rounded-umbo larvae, 165–195 μm ; knobby umbo larvae, larger than 200 μm . Eyespots and a well-developed active foot were first observed in larvae larger than 230 μm . Larval developmental rates at 20 ± 1 and $24 \pm 1^\circ\text{C}$, hinge structure characteristics, and a three-dimensional growth diagram are included.

INTRODUCTION

Modiolus capax Conrad, 1837, the fat horse mussel, may be found intertidally, where it forms clusters on rocks or boulders, or dredged in mud to 46 m. Its geographic distribution extends from central California, USA, to Peru, including the Galapagos Islands and the Gulf of California (SMITH & CARLTON, 1975; BRUSCA, 1980; MEINKOTH, 1981). *Modiolus capax* is not commercially exploited, but its widespread distribution in the eastern tropical Pacific, where the genus *Mytilus* is not present (KEEN, 1971), has recently stimulated interest in this mussel as a possible candidate for aquaculture or as an indicator of marine pollution.

Pollution by heavy metals and chloride hydrocarbons along the west coast of the Gulf of California has already been assessed using natural populations of *Modiolus capax* (VILLAESCUSA-CELAYA, 1987; GUTIÉRREZ-GALINDO *et al.*, 1988; ESPINOZA-OLGUÍN, 1989; DA COSTA-GÓMEZ & VALLE-DÍAZ, 1989). Also in recent years some aspects of its biology related to feeding, metabolism, reproductive cycle, and natural spatfall availability were investigated (OCHOA-BÁEZ, 1985; ORDUÑA-ROJAS, 1986; RICO-MORA, 1987; MAZÓN-SUÁSTEGUI, 1987; AGUIRRE-HINOJOSA, 1987; ESPINOZA-PERALTA, 1989; GARZA-AGUIRRE & BÜCK-

KLE-RAMÍREZ, 1990a, b). The present work describes a reliable procedure for the artificial spawning of *M. capax* and provides information on its developmental morphology from fertilization to the pediveliger stage and developmental rates at two temperatures.

MATERIALS AND METHODS

Samples of adult *Modiolus capax* (90 ± 11 mm in length) were collected monthly from February through September 1985, from a natural population in Bahía de Los Angeles, Baja California, Mexico ($28^\circ 53' 33''\text{N}$, $113^\circ 31' 30''\text{W}$). The mussels were taken to the laboratory, cleaned of any epibiotic growth, and kept in lots of 25 in 40-L aquaria with seawater at 36 ± 1 ‰ and $20 \pm 2^\circ\text{C}$. Water renewal and feeding were done three times a day to provide an approximate daily ration of *Pavlova* (*Monochrysis*) *lutheri* (Droop) Green equivalent to 0.5% of the mussel's soft body tissue. The rations were calculated using an average dry weight of 28 pg/cell of *P. lutheri* and 2.5 g of dry soft body tissue/mussel, values estimated in the laboratory with eight nonaxenic *P. lutheri* cultures and 10 mussels. Feeding was discontinued 24 hr before the spawning inducement, which was performed no more than 18 days after collection.

A sample of 10 to 15 mussels was used to estimate an

average gonadic index (GI) based on wet weights (± 0.001 g) of the gonad central body (GW) and total soft body tissue (TW) according to the formula $GI = (GW/TW) \times 100$. Although from February to April the gonadic index was low ($<20\%$), specimens were used in lots of 25 to test the following spawning stimuli: air exposure, thermal shock, gradual increase in water temperature, potassium chloride immersion, addition of gametes to the water, and mechanical shock (IWATA, 1951; LOOSANOFF & DAVIS, 1963). Also, different combinations of these stimuli were tested. All the spawning trials lasted 3.5 hr.

Fertilization was carried out at 24°C with the spawned products from at least two males and two females. Prior to this, the obtained ova were allowed to hydrate in clean seawater, also at 24°C , from 1 to 2 hr. The addition of 3 mL of a dense sperm suspension to a 4-L suspension of ova was followed by gentle agitation of the mixture, allowing 5 min to complete fertilization. The eggs were washed through a $56\text{-}\mu\text{m}$ sieve and transferred to 40-L aquaria containing UV sterilized seawater (36‰ , $24 \pm 1^\circ\text{C}$); their density was adjusted to 150 eggs/mL. At 10-min intervals during the first 3 hr and every hour afterwards, embryonic development was checked under an Olympus BHT dissecting microscope equipped with a camera.

Larval culturing at 20 ± 1 and $24 \pm 1^\circ\text{C}$ was also carried out in 40-L aquaria with an initial concentration of 15 larvae/mL. These cultures were supplied with aeration and the microalga *Pavlova lutheri* in concentrations of 10^5 cell/mL. Every other day the water was changed, the larvae were examined, photographed and measured, and a sample of organisms preserved in a fixative described by CULLINEY *et al.* (1975). Values of total length, height, and depth obtained from the preserved larvae were used to construct a three-dimensional growth diagram as described by CHANLEY & VAN ENGEL (1969). An JSM5300 scanning electron microscope was used to examine the hinge structure of selected larval stages.

RESULTS AND DISCUSSION

Spawning

During the spawning trials, we noted that a combination of air exposure, mechanical stimulation, and thermal stimulation invariably elicited in the mussels mucus secretions and a vigorous flow from the exhalant region. Similar behavior in other mussel species is indicative of strong stimulation and usually precedes spawning. Thus, no further attempts were made with the other stimuli nor to improve or simplify the technique. The successful procedure consisted of exposing the specimens to air for 6 hr, scraping their valves, and transferring them to a 70-L rectangular, fiberglass tank with recirculating seawater at 27°C . If a subsequent increase in water temperature to 29°C (accomplished over a 2-hr period) did not initiate spawning, stripped gametes (preferably ova) were added

to the water and the temperature was increased to 30°C over the course of an hour.

Using this procedure, spawning was induced for the first time in early May with a spawning efficiency ratio (organisms spawned/organisms tested) of 5/25. This ratio was 8/25 in June, 18/25 in July, 90/190 in August, and 8/25 in September. The monthly averages in the gonadic index of *Modiolus capax* were consistent with these results: below 20% from February to April when no spawnings were obtained, highest in July and August ($32 \pm 5\%$) when the spawning efficiency ratio was maximum, and sharply lower ($<15\%$) in September when the spawning ratio also declined. These results are in fair agreement with the reproductive cycle described by OCHOA-BÁEZ (1985) for a population of *M. capax* from La Paz, B.C.S., Mexico, a location approximately 750 km south of our collecting site. According to that study, *M. capax* shows no sexual activity in late autumn and winter, but has continuous gonadal activity from spring to early autumn, with a first spawning peak in April and a second, very intense one, in July–August. In this location, the water temperature range is $22\text{--}29^\circ\text{C}$; in Bahía de Los Angeles it is $14\text{--}29^\circ\text{C}$. In both sites the minimum and the maximum temperature occur in February and August, respectively.

A detailed study of the reproductive cycle of the *Modiolus capax* population from Bahía de Los Angeles, using histological analysis of the gonads, later confirmed this spawning season (GARZA-AGUIRRE & BÜCKLE-RAMÍREZ, 1990a). However, in contrast to OCHOA-BÁEZ (1985) these authors found some gonadal activity during late autumn and winter. Later work (still in progress) on the artificial spawning of *M. capax* has shown that during this period a fraction of the population may spawn, though an additional thermal shock may be necessary. The spawning organisms are mainly males, however, while females usually discharge gonadal tissue and a small quantity of ova, which is consistent with the reduced gonadal volume found during this period.

The spawning mechanisms observed in *Modiolus capax* were comparable to those described in other mussels (BAYNE, 1978). In neither sex is the deposition of gametes accompanied by valve contractions. The sperm flows out of the valves in a continuous milky stream propelled by currents of the exhalant region. In females the process is similar. The bright orange ova flow out in a scattered stream or in short disconnected bands.

The spermatozoa have an oval head ($4 \times 3\text{ }\mu\text{m}$) with a small protuberance in the anterior region and two posterior spherical bodies less than $1\text{ }\mu\text{m}$ in diameter. The tail is $41\text{--}44\text{ }\mu\text{m}$ long. The ova are spherical, $70\text{--}81\text{ }\mu\text{m}$ in diameter, and have no visible nucleus.

Embryological Development

At 24°C , the egg extrudes the first polar body 3–5 min after fertilization. The second polar body appears underneath this within 5–10 min of fertilization (Figure 1A).

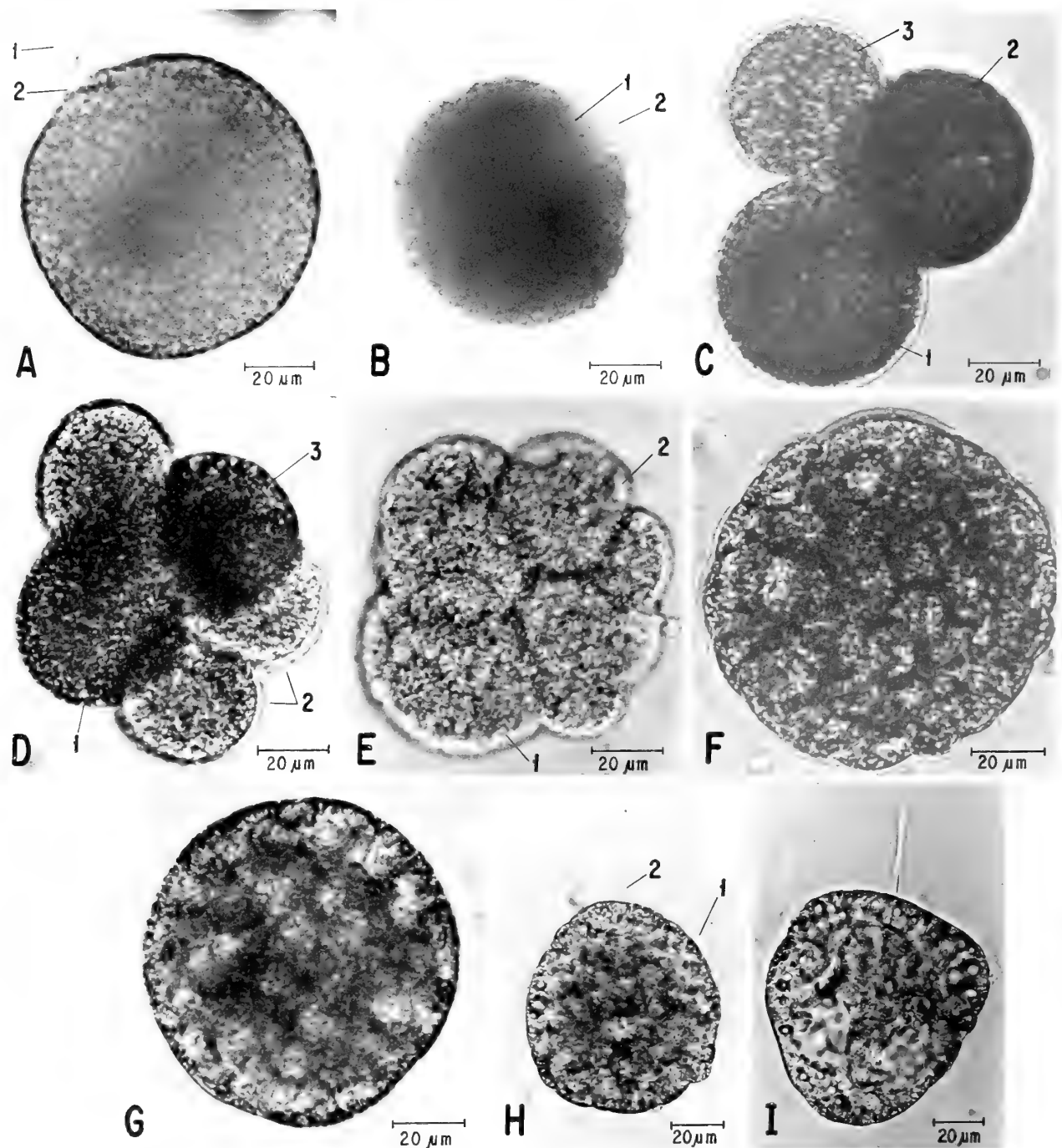


Figure 1A-I

Embryological development of *Modiolus capax*. A. Egg with first (1) and second (2) polar bodies. B. Egg prior to first division showing ooplasmic segregation (1) and enlarged perivitelline space (2). C. First division in progress: vegetative pole (1), animal pole (2), and polar lobe (3). D. Second division in progress: macromere (1), micromeres (2), and polar lobe (3). E. Embryo product of third division showing macromere (1) and micromeres (2). F. Morula stage. G. Ciliated gastrula. H. Early trochophore showing cilia (1) and flagellum (2). I. Late trochophore.

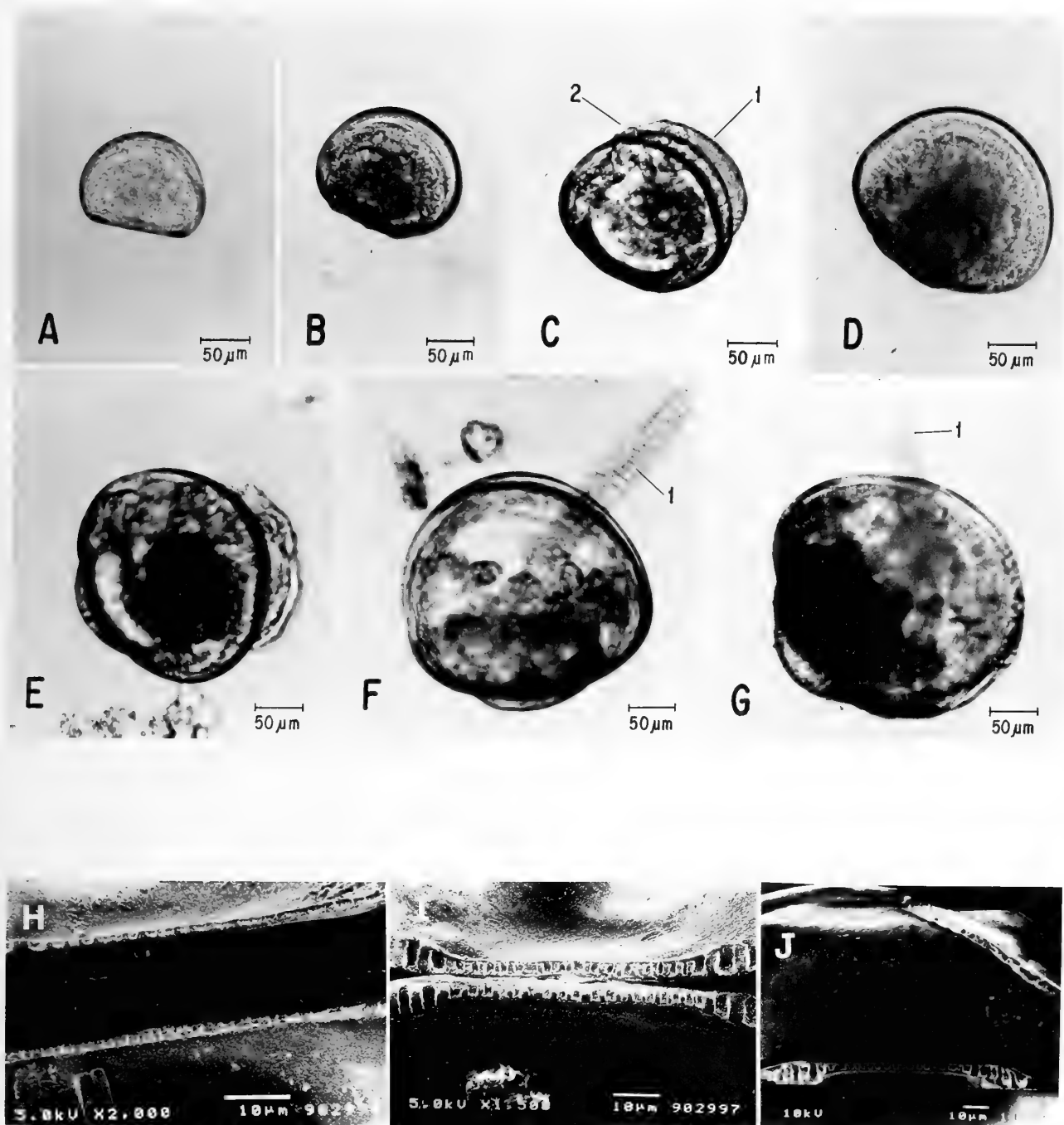


Figure 2A-J

Photomicrographs of *Modiolus capax* larvae and scanning electron micrographs of hinge structures of selected larval stages. A and B. D-shaped larvae, with corresponding lengths of 129 and 156 μm. C. Round-umbo stage: 178 μm long larva showing velum (1) and incipient foot (2). D and E. Umboned larvae: corresponding lengths of 220 and 250 μm. F and G. Pediveligers showing well-developed, active foot (1), corresponding lengths of 275 and 290 μm. H. Hinge structure of newly shelled straight-hinge larva. I. Hinge structure of round-umbo larva. J. Hinge structure of umboned larva.

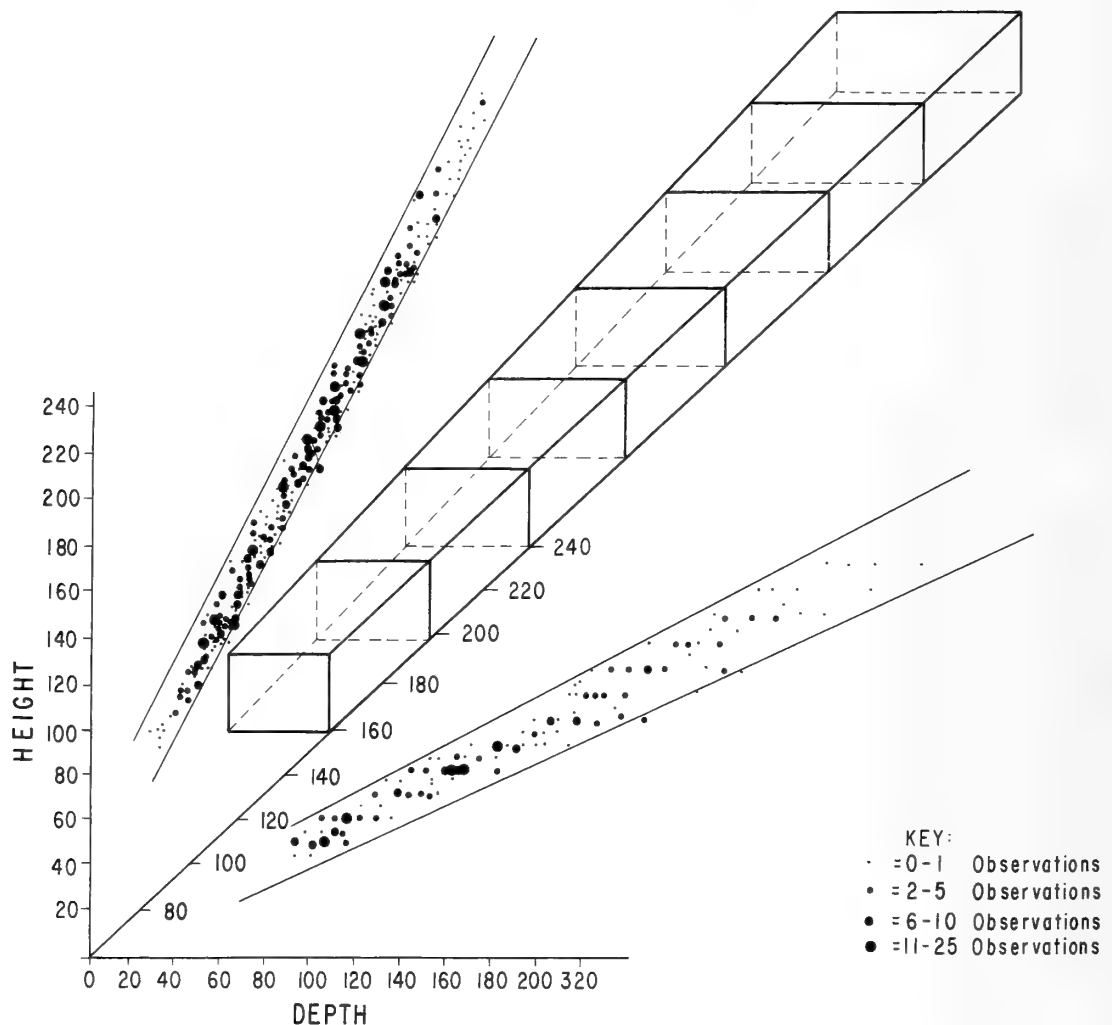


Figure 3

Larval dimensions of *Modiolus capax*. Three-dimensional diagram showing polyhedron encompassing all possible length-depth-height combinations of *M. capax* larvae and two-dimensional graphs of height-length and length-depth observations. Figure constructed according to the procedure described by CHANLEY & VAN ENGEL (1969).

During the next 20–30 min, ooplasmic segregation toward the center of the egg leaves a conspicuous perivitelline space, and the vitelline membrane becomes wavy in outline (Figure 1B).

During the first cleavage, a polar lobe is formed, producing in this way the trefoil stage shown in Figure 1C. The two-cell stage, reached 50–70 min after fertilization, has unequally sized blastomeres. As shown in Figure 1D, the second cleavage is also unequal and accompanied by polar lobe formation. The four-cell stage has three micromeres and one macromere, with their nuclei visible as round clear spots in the center of the cells. This stage is reached 80–90 min after fertilization. The following two cleavages occur within the next 50 min. The resulting embryos also show a cup of micromeres over a single macromere (Figure 1E), which becomes enveloped by the

micromeral cells as cell multiplication proceeds. The morula (Figure 1F) was first observed 2.5 hr after fertilization and lasted a few minutes.

The gastrula stage was observed 7 hr after fertilization (Figure 1G). As in *Mytilus edulis* (FIELD, 1922) it has short, fine cilia over its entire surface and moves slowly. General descriptions of development in other *Modiolus* species are restricted to larval stages and provide no information regarding their cleavage pattern and early development (LOOSANOFF *et al.*, 1966; CHANLEY & ANDREWS, 1971; DE SCHWEINITZ & LUTZ, 1976). Given the type of process described earlier, it seems probable that gastrulation and germ layer formation are similar to those of *Mytilus edulis*. In this species, gastrulation is by epiboly and invagination: the mesoderm arises from the macromere that is ultimately surrounded by the micromeral cells, the

ectoderm from the micromeres situated on top, and the endoderm from the invagination of micromeres that come to lie in the region of the vegetative pole.

Larval Development

In the early trochophore of *Modiolus capax*, observed 9 hr after fertilization, the cilia have grown larger, especially in the anterior region where a long flexible flagellum composed of three filaments has also developed (Figure 1H). At this stage, swimming is forward in a spiral motion. During the next 10 hr, the larvae experience a general thickening of the ectoderm and become triangular in shape (Figure 1I). A further thickening of the dorsal ectoderm forms the shell gland and the embryonic shell soon appears as a thin integument over the gland. As shell secretion continues, the anterior region of the embryo enlarges to form the velum.

A typical straight-hinge larva was observed 24 hr after fertilization. The newly shelled, straight-hinge larvae measure, on average, $105 \pm 8 \mu\text{m}$ in length, $85 \pm 8 \mu\text{m}$ in height, and $53 \pm 6 \mu\text{m}$ in depth. The hinge line is $88 \pm 3 \mu\text{m}$ long; scanning electron micrographs revealed 18 small central hinge teeth and two larger ones on each side (Figure 2H). As in *Modiolus modiolus* (DE SCHWEINITZ & LUTZ, 1976) and *M. demissus* (LOOSANOFF *et al.*, 1966) the straight-hinge form in *M. capax* persists to an approximate length of $160 \mu\text{m}$ (Figure 2A, B). At this larval size the hinge line is $93 \pm 3 \mu\text{m}$ long, and the hinge teeth are stronger and increased by one on each side (Figure 2I). The umbo appears as a rounding of the hinge line (Figure 2C), becoming more conspicuous and broadly round in larvae larger than $200 \mu\text{m}$ (Figure 2D–G). With growth the hinge teeth increase further in size and number; the umboned larvae have four large teeth at each end of the hinge line (Figure 2J). In larvae reared at $24 \pm 1^\circ\text{C}$, the round-umbo stage was first observed the sixth day of culture and the umbo stage on day 12.

Eyespots (on average $8 \mu\text{m}$ in diameter) and a well-developed, active foot were first observed in larvae larger than $230 \mu\text{m}$ in length. In pediveligers of *Modiolus capax* larger than $270 \mu\text{m}$ (first observed on day 18 of culture at 24°C), the foot, when fully extended, is almost as long as in larvae that are apparently fully competent for settlement (Figure 2G, H). By contrast, in *M. modiolus*, pigmented eyespots first appear in larvae exceeding $270 \mu\text{m}$ in length, and a full-grown, functional foot appears in larvae larger than $295 \mu\text{m}$ (DE SCHWEINITZ & LUTZ, 1976).

First-shelled larvae transferred from water at 24°C to $20 \pm 1^\circ\text{C}$ had comparable mortality rates (55%) to those kept at 24°C during the first seven days of culture. At the lower temperature, however, mortality increased sharply thereafter, and larval growth was negligible. Larvae attained a maximum length of $150 \mu\text{m}$, first registered on the eighteenth day of culture.

A data set of 670 length-height measurements from veligers in all stages of development yielded the linear re-

gression equation: $\text{height} = 0.913 \times \text{length} - 14.0$ ($r^2 = 0.95$). The same calculation for 280 length-depth measurements yielded the relationship: $\text{depth} = 0.978 \times \text{length} - 57.0$ ($r^2 = 0.86$). Both sets of data were used to construct the three-dimensional diagram of Figure 3, showing the polyhedrons encompassing all length-height-depth combinations found throughout larval development.

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A New Species of *Mopalia* (Polyplacophora: Mopaliidae) from the Northeast Pacific

by

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Abstract. A new species of chiton, *Mopalia ferreirai*, is described from the shallow subtidal waters (0-18 m) of the Pacific coast of North America. Specimens are of medium size for the genus and resemble *Mopalia spectabilis* Cowan & Cowan, 1977, but differ in the structure of the girdle hairs.

INTRODUCTION

For many years an undescribed species of the genus *Mopalia* Gray, 1847, has been known to malacologists in the Pacific Northwest. It has often been erroneously identified as *Mopalia swanii* Carpenter, 1864, *M. spectabilis* Cowan & Cowan, 1977, or *M. lowei* Pilsbry, 1918, to which it is closely related. On recent trips to southeastern Alaska I have collected many specimens of this species. An examination of these along with other specimens from throughout the region (Alaska to central California) confirmed that it was indeed a new species, which is described here.

Abbreviations used in text are LACM, Los Angeles County Museum of Natural History; USNM, United States National Museum of Natural History, Washington, DC; CAS, California Academy of Sciences, San Francisco; SBMNH, Santa Barbara Museum of Natural History; ZIAS, Zoological Institute, Academy of Sciences, Leningrad; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; ANSP, Academy of Natural Sciences, Philadelphia; RNC, private collection of Roger N. Clark; BMNH, British Museum of Natural History, London.

TAXONOMY

Class POLYPLACOPHORA Gray, 1821

Order NEOLORICATA Bergenhayn, 1955

Family MOPALIIDAE Dall, 1889

Genus *Mopalia* Gray, 1847

Type species: *Chiton hindsii* Reeve, 1847.

Mopalia ferreirai Clark, sp. nov.

(Figures 1-5, 12, 13)

Mopalia lowei, non Pilsbry: BURGHARDT & BURGHARDT, 1969: cover, pl. 4, no. 62, 63; SMITH, 1977:251 (from Sitka, Alaska).

Diagnosis: Chitons of medium size (up to 5 cm), variably colored, carinate, beaked; tegmentum microgranular; central areas reticulate; lateral areas weakly elevated, well defined and finely beaded; mucro posterior one-third. Girdle moderately wide (about one-half the width of valve five), armed with short, very spinose setae. Radula mopalioid, with large tricuspid major laterals.

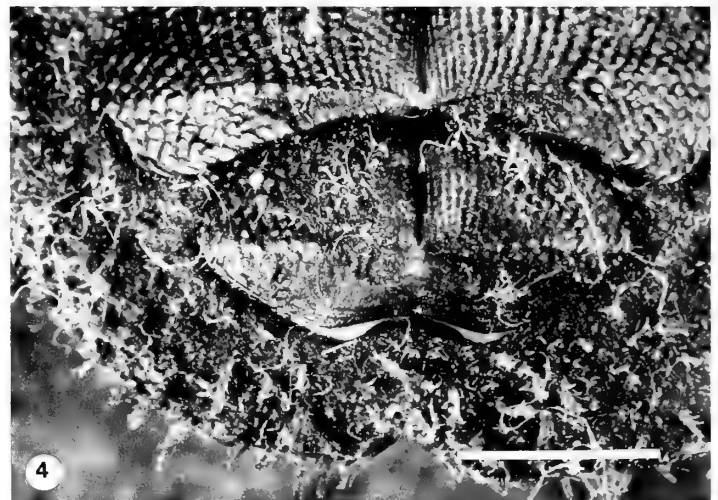
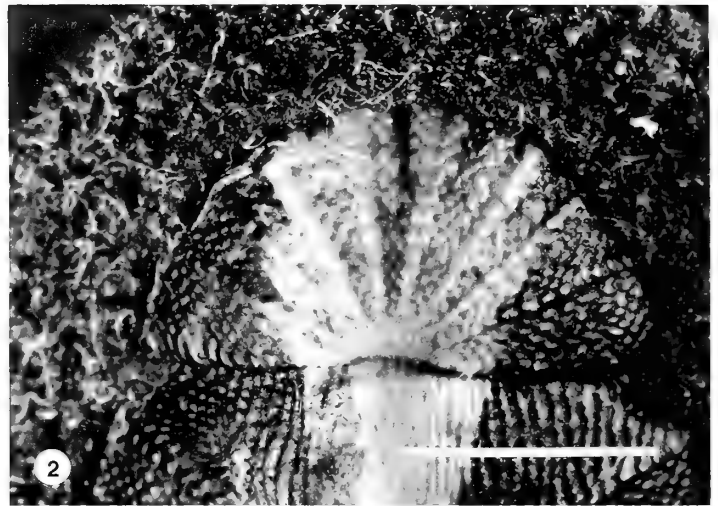
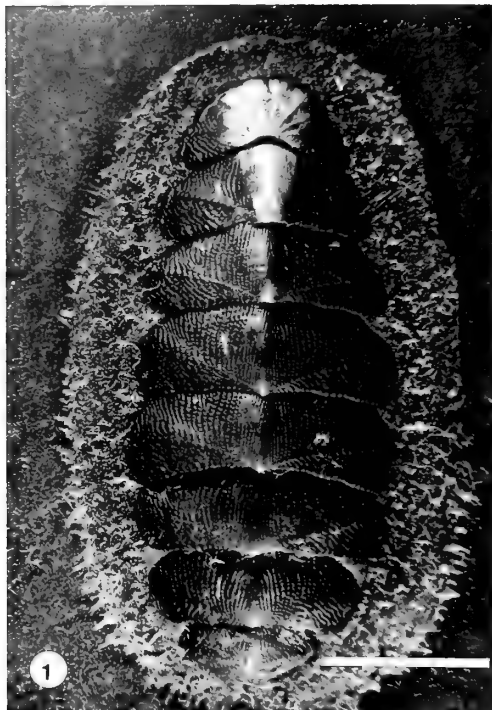
Type material: Holotype (LACM 2329) and 18 paratypes (3, LACM 2330); (2, CAS 069315); (1, SBMNH 35141); (2, USNM 860484); (1, ZIAS 1931); (2, UMMZ 252311, 252312); (1, RMNH 9236); (1, ANSP A-13392); and 5 in the collection of the author (RNC 269, 538).

Holotype and 11 paratypes are preserved dry (with glycerin), flat, and fully extended; collected 17 August 1986 by R. N. Clark. Seven additional paratypes, also flat and fully extended, are preserved in 70% isopropyl alcohol; collected 28 August 1990.

Type locality: Rotary Beach, 5 km S of Ketchikan, Revillagigedo Island, Alaska (55°16'N, 131°34'W), 0.5 to 1 m, on the bottoms of large rocks.

Description: Holotype (Figures 1-4) dry preserved, flat, fully extended; dimensions (including girdle) 41.0 mm in

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Explanation of Figures 1 to 4

Figures 1-4. *Mopalia ferreirai* Clark, sp. nov., holotype.

Figure 1. Whole animal (dorsal view), bar = 1 cm.

Figure 2. Anterior valve, bar = 5 mm.

Figure 3. Intermediate valves ii-iv (left side), bar = 3 mm.

Figure 4. Posterior valve, bar = 4 mm.

length, 24.0 mm in width, and 7.0 mm in elevation; jugal angle about 110° ; valves carinate, moderately elevated, and slightly beaked. Color overall reddish-brown, with yellowish tint on older portion of shell; central portion of anterior valve, and jugum of second valve white. Anterior valve (Figure 2): 11.0 mm in width and bearing 10 rows (2 marginal and 8 intermediate) of low, rounded pustules, about 14 in a series (apex eroded); interstices with 3–8 radiating rows of low, smooth pustules. Intermediate valves (Figure 3): valve five 16.0 mm in width and 8.0 mm in length (including sutural laminae); central areas with 22–24 longitudinal ribs per side of jugum, transversed by smaller, slightly upwardly diverging ribs giving fine but crisp pitted appearance; lateral areas very slightly raised, defined by one row of pustules similar to those on anterior valve; surface of lateral areas with 8–10 staggered, radiating rows of low, smooth pustules; posterior margin of valves with backwards and slightly upwardly directed elongate-oval pustules. Posterior valve (Figure 4): 10.0 mm in width (tegumentum 8.5 mm in width) and 6.0 mm in length (including sutural laminae); mucro posterior one-third and raised; premucronal area with 18 longitudinal ribs crossed by much finer (nearly obsolete) transverse ribs; postmucronal area obsoletely sculptured like lateral areas. Articulamentum translucent white, tinted with faint blue-green at apices. Slit formula typical for genus, 8/1/2, slits in posterior valve separated by a moderately wide caudal sinus; sutural laminae moderately long and rounded; insertion teeth long and well formed, and bearing fine vertical striations on outside surface. Girdle (Figure 5): moderately wide, about 4.5 mm at valve five, moderately encroaching at sutures, light brown; covered with very fine spicules up to $150\ \mu\text{m}$ in length, occurring singly or in groups of up to 10, and with tiny scales that are striated along the upper one-fourth; scales on dorsal surface measuring $45\ \mu\text{m}$ in length and $8\ \mu\text{m}$ in width, those on ventral surface measuring $80\ \mu\text{m}$ in length and $12\ \mu\text{m}$ in width; girdle also bearing short (up to 2.0 mm), flattened setae armed with numerous rows of chitinous bristles, generally three rows on dorsal surface and one each on lateral surfaces. Radula (Figure 12): preserved separately, in 70% isopropyl alcohol, 13 mm in length and bearing about 28 mature rows of teeth; central tooth rectangular, though somewhat tapered on the lower one-third, $300\ \mu\text{m}$ in length, cutting edge about $150\ \mu\text{m}$ in width; minor lateral teeth triangular, about $300\ \mu\text{m}$ in length; major laterals very large, about $800\ \mu\text{m}$ in length and bearing one large tricuspid head about $300\ \mu\text{m}$ in length and $180\ \mu\text{m}$ in width, central cusp the largest, inner cusp slightly smaller, and outer cusp slightly more than one-half length of central one; first marginal teeth large and angular, bearing large hornlike projection on inner lateral margin, dimensions $350\ \mu\text{m}$ by $260\ \mu\text{m}$; spatulate (third) marginal teeth large, about $625\ \mu\text{m}$ in length and $75\ \mu\text{m}$ in width; outer marginals rounded, diamond shaped, about $430\ \mu\text{m}$ in length and $210\ \mu\text{m}$ in width. Gills merobranchial, abanal, extending three-fourths length of foot; about 30 plumes per side.

5

6



1.0mm



1.0mm

7

8



1.0mm



1.0mm

Explanation of Figures 5 to 8

Figure 5. *Mopalia ferreirai* Clark, sp. nov. (Annette Id., Alaska; RNC 867). Single seta with bristles.

Figure 6. *Mopalia swanii* Carpenter, 1864 (Neah Bay, Washington; RNC 202). Single seta with bristles.

Figure 7. *Mopalia spectabilis* Cowan & Cowan, 1977 (Coos Bay, Oregon; RNC 354). Single seta with bristles.

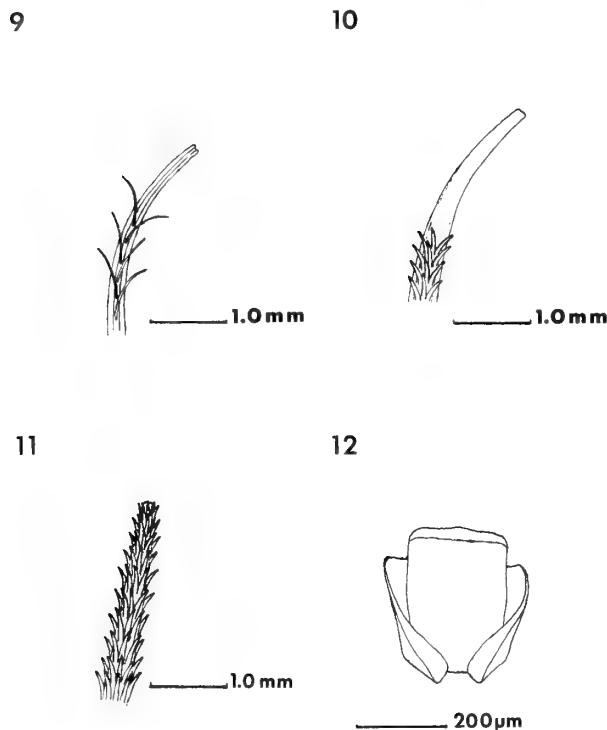
Figure 8. *Mopalia acuta* (Carpenter, 1855) (Point Conception, California; RNC 444). Single seta with bristles.

Variation: Girdle: In some specimens the setae bear a few spines on the ventral as well as the dorsal and lateral surfaces, but this is rare.

Coloration: The tegmental coloration may be uniform or nearly uniform rose, violet, light blue, green, yellow, reddish-brown, or orange. Alternatively, it may be maculated with these colors or with black, tan, white, or brown. Some specimens have one or more unicolored valves and the rest varicolored. A common variant has a blue-green ground color maculated with reddish-brown and occasionally white.

Distribution: *Mopalia ferreirai* has been found continuously between latitudes 60°N (Prince William Sound, Alaska) and 36°N (Carmel Bay, Monterey County, California) (Figure 13) and from a bathymetric range of +0.5 m in the north to at least 18 m in the southern portion of its geographic range. It is usually found on the bottoms of large rocks.

Etymology: Named in honor of the late Dr. Antonio J.



Explanation of Figures 9 to 12

Figure 9. *Mopalia seta* Yakovleva, 1952 (Sea of Japan; RNC 482). Single seta with bristles.

Figure 10. *Mopalia ciliata* (Sowerby, 1840) (Point Conception, California; RNC 208). Single seta with bristles.

Figure 11. *Mopalia lowei* Pilsbry, 1918 (Shell Beach, California; RNC 288). Single seta with bristles.

Figure 12. *Mopalia ferreirai* Clark, sp. nov., holotype. Central and minor lateral teeth.

Ferreira, who greatly expanded our knowledge of this fascinating group of mollusks.

DISCUSSION

Because of the taxonomic confusion associated with the genus *Mopalia*, it was necessary to examine the type material (either directly or via photographs) of as many of the similar-appearing species as could be obtained. These were as follows: *Mopalia lowei* Pilsbry, 1918 (ANSP 117951), *Mopalia spectabilis* Cowan & Cowan, 1977 (paratype RNC 223, ex I. McT. Cowan 10593), *Chiton acutus* Carpenter, 1855 (holotype, BMNH 61.5.20.103; illustrated by PALMER, 1958:pl. 31, fig. 18).

The type of *Mopalia swanii* Carpenter, 1864, is lost (PALMER, 1958:283), and present identifications of this species are based on BERRY (1951:214–217, 219, pl. 26, fig. 15). The type of *Chiton ciliatus* Sowerby, 1840, was not examined because the original description (republished by Pilsbry in 1892) is adequate for recognizing this species. The type of *Mopalia seta* Yakovleva, 1952, is at the ZIAS,

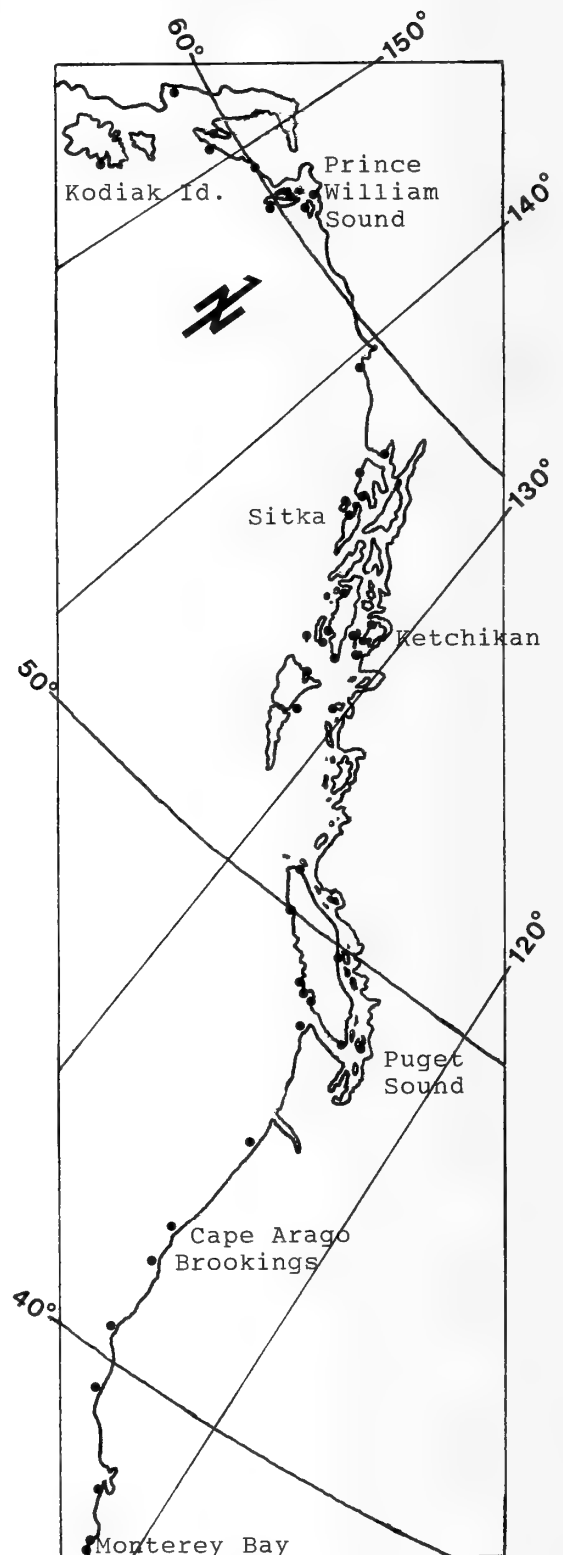


Figure 13

Mopalia ferreirai Clark, sp. nov. Distribution map.

and was not examined, but Dr. B. I. Sirenko of that institution provided me with four specimens of this species (all collected and identified by him) that agree very well with the original description.

On the basis of seta structure, *Mopalia ferreirai* belongs in the same species group as: *M. acuta* (Carpenter, 1855), found from central California to Baja California Norte, Mexico; *M. swanii* Carpenter, 1864, found from Unalaska Island, Alaska, to Malibu, California; *M. spectabilis* Cowan & Cowan, 1977, found from Kodiak Island, Alaska, to Point Conception, California; and *Mopalia seta* Yakovleva, 1952, which is restricted to the Sea of Japan. This group is characterized by thick setae (0.5 to >1.0 mm in width at the base in specimens over 25 mm in length) bearing chitinous bristles. This group is clearly distinct from the group—comprised of *Mopalia ciliata* (Sowerby, 1840), found from Kamchatka to Baja California Norte, Mexico, and *M. lowei* Pilsbry, 1918, found from Bodega Bay, California, to Baja California Norte, Mexico—characterized by thick setae (0.5 to >1.0 mm in width at the base in specimens over 25 mm in length) bearing calcareous spines. These two groups were separated by immersing the setae from each species in a solution of hydrochloric acid, which dissolves calcareous spines. This difference in setal composition is regarded as a provisional indication that the *M. acuta* and *M. ciliata* groups are natural assemblages, but this view awaits additional corroboration.

Mopalia ferreirai may be distinguished from the other four members of the *M. acuta* group by the presence of short, flattened (sometimes slightly trough-shaped) setae bearing three rows of short, thick, curved bristles on the dorsal surface and one row each on the lateral surfaces. All other members of the *M. acuta* have strongly trough-shaped setae. *Mopalia acuta* (Figure 8) has one row of long, fine, curved bristles originating in the trough; *M. swanii* (Figure 6) has two rows of long, curved bristles, one each originating on the inner lateral surface of the setae; and *M. spectabilis* (Figure 7) has very long setae (up to 6.0 mm in length) bearing five rows of very long (up to 1.0 mm), curved bristles. In *M. seta* the trough is reduced to a narrow groove from which arises a single row of very long, fine, curved bristles.

Mopalia ciliata (Figure 10) has flattened or slightly trough-shaped setae that are usually strongly recurved, and bear three rows of short, stout, white spines, not extending beyond one-half the length of the seta. *Mopalia lowei* (Figure 11) has long (up to 5.0 mm) thick, tapering, shaftlike (round) setae bearing rather short, sharp spines all the way around the axis, about 6–9 per axil row (increasing in number with the size of the seta).

Mopalia ferreirai and *M. lowei* are superficially similar, particularly in the spinose appearance of their setae. But the tegmental sculpture of *M. lowei* is much stronger. Also, the spines of *M. lowei* (and *M. ciliata*) are white, whereas the spines of *M. ferreirai* and all of the members of the *M. acuta* group are light brown, golden, or tan.

ACKNOWLEDGMENTS

Much thanks and appreciation are due the following people for their help and encouragement: the late Dr. Antonio J. Ferreira, who started me on this project; Col. George A. Hanselman of San Diego, California, for his excellent photographs and for critical reading of early manuscripts; Rae Baxter of Red Mountain, Alaska, for sending many specimens and data; Dr. Ian McTaggart Cowan of Victoria, British Columbia, for lending many specimens and providing additional data; Gordon Green of the Royal British Columbia Museum, Victoria, for the loan of specimens; Dr. James T. Carlton (formerly of the Oregon Institute of Marine Biology) for making his facilities available to me and for help on the manuscript; Dr. James H. McLean, Los Angeles County Museum of Natural History, for his help and encouragement and for critical reading of the manuscript; Thomas C. Rice, of Sea & Shore Museum, Port Gamble, Washington, for his help and encouragement; Lindsey Groves, Los Angeles County Museum of Natural History, for help with the literature search; Dr. Douglas J. Eernisse, University of Michigan Museum, for his helpful comments; Dr. B. I. Sirenko of the Zoological Institute, Academy of Sciences, Leningrad, for sending specimens of *Mopalia seta*; Elizabeth Kools, California Academy of Sciences, for her help; David S. Wieder of the Academy of Natural Sciences in Philadelphia for sending photographs of the type specimen of *M. lowei*; Graham and Sue Jeffrey and George P. Holm of Vancouver, British Columbia, and Elsie Marshal and William E. Rice of Seattle, Washington, for making their specimens and collecting notes available to me. The evaluations of two anonymous reviewers greatly enhanced this paper.

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NOTES, INFORMATION & NEWS

International Commission on Zoological Nomenclature

The following applications were published on 20 December 1990 in Volume 47, Part 4 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2768—*Lepidomenia* Kowalevsky in Brock, 1883 (Mollusca: Solenogastres): proposed designation of *Lepidomenia hystrix* Marion & Kowalevsky in Fischer, 1885, as the type species.

Case 2739—*Helicarion* Férussac, 1831 (Mollusca: Gastropoda): proposed conservation, and proposed designation of *Helicarion cuvieri* Férussac, 1821, as the type species.

Case 2588—*Haminaea* Leach, [1820] (Mollusca: Gastropoda): proposed conservation.

Case 2670—*Kobeltia* Seibert, 1873 (Mollusca: Gastropoda): proposed confirmation of *Arion hortensis* Férussac, 1819, as the type species.

Meeting of the American Society of Zoologists 1991

The 1991 Meeting of the American Society of Zoologists will be held from 27 to 30 December in Atlanta, Georgia. The meetings will be held in conjunction with the American Microscopical Society, Animal Behavior Society, The Crustacean Society, and The International Association of Astacology. Many symposia have been planned, includ-

ing—Libbie H. Hyman, Life and Contributions; Reproduction, Larval Development and Recruitment in the Deep-Sea Benthos; Long-term Dynamics of Coral Reefs; and The Biology of Flatworms.

The deadline for abstracts is 1 August 1991 if you wish to present a poster or oral paper.

For more information contact:

Mary Adams-Wiley, Executive Officer
American Society of Zoologists

104 Sirius Circle

Thousand Oaks, CA 91360

Phone: (805) 492-3585; FAX (805) 492-0370

Announcement: Royal British Columbia Museum

During 1991 and 1992, the Royal British Columbia Museum will be packing and moving their biological, anthropological, and historical collections to allow for removal of asbestos in their collections building. During this time some of their specimens and artifacts will be inaccessible. They will meet all existing commitments regarding loans and research access and will endeavor to meet any additional requests. Nevertheless, the necessary move will probably inconvenience users of the collection for much of 1991–1992.

For information on loans and research, contact:

Grant W. Hughes

Assistant Director, Collections Program

Royal British Columbia Museum

675 Belleville Street

Victoria, B.C.

Canada V8V 1X4

BOOKS, PERIODICALS & PAMPHLETS

**Antillean Seashells
The 19th Century Watercolours of
Caribbean Molluscs
Painted by Hendrik van Rijgersma**

by HENRY E. COOMANS. 1989. De Walburg Pers, P.O. Box 222, 7200 AE Zutphen, Holland. 192 pp., 74 color pls. + 6 text figs. + map endpapers. 8¼" × 5½". Hardback. ISBN 906011.616.X. U.S. \$24.00.

This is not an identification handbook, but it deserves a place in the history of West Indian marine malacology. Van Rijgersma (1835-1877) was a Dutch physician-naturalist stationed intermittently from 1863 until his death on the Dutch-French island of St. Martin in the northern Lesser Antilles. He delighted in collecting shells, observing the living animals, and recording some of what he saw with watercolors. (He did the same with flowering plants, the subject of a companion book by H. E. Coomans and M. Coomans-Eustatia.) Van Rijgersma was careful to record whether his observations and paintings were made on St. Martin or on another nearby island that he visited. A few of his illustrations are copies (the radulae), but there are admittedly somewhat amateurish original renditions of the mainly large shells of some of the conchs, cowries, helmets, and cymatiums, *etc.*, that one would expect to find in the West Indies.

The color plates illustrate 75 species (excluding the few copied from others). There are surprises such as six turrid species, not usually paid heed by the average collector, and the only good published illustrations known to me of the opercula of *Strombus gigas* and *Cassis madagascariensis* (but the last should be brown, not white). Many of the shells are life size, so that four trivias on one plate have come out as small, almost meaningless blobs. But there are nine species showing the living animals—the most unexpected being *Strombus gallus*. I am sure that there is no other color picture of this animal in the literature. Not to be overlooked are the observations in the text, which when originally in Dutch have been translated into English. Van Rijgersma noted the pearls of *Strombus gigas*.

Dr. Henry E. Coomans, a malacologist at the Zoologisch Museum, Amsterdam, has long been interested in Caribbean malacology and van Rijgersma. In 1974 Coomans published in *Bijdragen tot de Tierkunde* his doctoral thesis—a scholarly study of van Rijgersma's malacological manuscripts and illustrations. At that time, the paintings could only be published in part and in black-and-white. Now we have all of them in splendid color, in a book appropriately written by Coomans himself. The taxonomy is up-to-date (but one could quibble about a few of the names). *Morum* is correctly placed in the Harpidae. The book is usefully rounded out with a biography of van

Rijgersma, a history of malacological research in the Netherlands Antilles, and a chapter on Rijgersma and malacology, all by Coomans. There is a good bibliography and an index.

Van Rijgersma's manuscripts are now in the Archives of the Academy of Natural Sciences of Philadelphia.

Robert Robertson

**Weichtiere: Europäische
Meeres- und Binnenmollusken**

by ROSINA FECHTER & GERHARD FALKNER, edited by Gunter Steinbach, illustrated by Fritz Wendler. 1990. 288 pp., 740 color photographs, 13 drawings. Steinbachs Naturführer, ISBN 3-570-03414-3. Mosaik Verlag GmbH, Neumarkter Str. 18, D-8000 München 80, Germany. Price: DM 29.80.

This German publication, neatly produced in the form of a hard-bound, small-octavo volume, has just appeared in the series of Steinbach's nature guides (other volumes cover topics ranging from orchids to minerals). The title *Weichtiere* (mollusks) becomes more narrowly focused in the subtitle, which promises European marine and non-marine mollusks.

No, this is not just another pretty-picture-guide for the beginning shell collector. Some technical data: this work presents 660 species, almost half of them documented by color photographs of living animals. A general introduction to Mollusca and its classes is given. In addition to the main groups Gastropoda and Bivalvia, the guide covers eight species of Polyplacophora, five of Cephalopoda, and one of Scaphopoda. Common (German) and Latin names, descriptions, chapters on distribution, habits and habitat, and often reproduction are arranged on pages adjacent to the photographs. No page leafing is required to match text and figures. To conserve space in the descriptive part, several abbreviations are used. These are explained on the verso of the title page (p. [4]). The reader not very familiar with the German language may find a translation useful: A = Atlantic Ocean, M = Mediterranean, N = North Sea, O = Baltic Sea, Ch = Characters, L = Habitat, D = Species occurs in West Germany [original Federal Republic], (D) = Species was introduced to West Germany, RL = Species is listed in German "red list" of endangered species. The appendix contains a brief system of the treated taxa (arranged by superfamilies), a description of one new taxon (see below), a glossary, suggestions for further reading, general hints for collectors, a source index for illustrations and figured specimens, as well as a comprehensive taxonomic index.

The general sections, introducing the phylum and classes, are informative but not always accurate. In cephalopods, the molluscan foot does not only form the tentacles (p. 11), but also the funnel. Molluscan gills can show other arrangements than the stated one-, two-, or fourfold conditions (p. 11). The sketch of the anatomical organization of a snail (p. 23) should have included a digestive gland. Also, the statement that there are only a few hermaphroditic bivalves (p. 72) is incorrect.

This work is especially noteworthy for its second part, *Binnenmollusken* (nonmarine [or more literal: landlocked] mollusks), written by Gerhard Falkner (pp. 112–280, including appendix). This section combines well-researched, concise text with excellent illustrations. The color photographs (480 species of land and freshwater mollusks, 279 of which are illustrated with the living animal) impress the reader by their quality and are also well documented with footnotes stating collecting region and exact scale. In addition to the illustration of taxonomic characters of shells and exposed soft parts, they provide a wealth of biological information. Polymorphism, feeding, mating, egg-laying, aestivation, hibernation, parasitism, and predation are only some of the topics well documented in text and photographs.

Space does not allow a list of all the highlights in this part. Whether it is the variation in shell and opercula of freshwater Neritidae (p. 115), the photographs of crawling individuals of Valvatidae (p. 121), Clausiliidae (pp. 154–165), and land slugs (pp. 184–199), of *Oxychilus draper-naudi* feeding on an earthworm (p. 180), or the underwater photographs of living unionids (p. 261), even the entrenched marine worker will be fascinated by this book. Many years of extensive literature and field research must have gone into the preparation of this section.

The marine part, written by Rosina Fechter (pp. 9–111, including the general section), is no match in comparison and looks like any other shell guide produced for the casual beach tourist. The editor (p. 7) found a somewhat peculiar explanation for the difference in quality and arrangement between the marine and nonmarine parts of the book. According to his conception, the beachcomber (*Strandgänger*) needs photographs of empty shells on neutral background for identification, while the nonmarine mollusks are best illustrated by photographs of living animals because they can be visited in their respective habitats. Come on, the North Sea and Mediterranean are not *that* cold! It is difficult to understand why common species like *Gibbula cineraria* (p. 31), *Littorina littorea* (p. 38), and

Turritella communis (p. 40) had to be illustrated by beach-worn shells. Unlike Falkner, who collected and photographed especially for this work, Fechter relied largely on photographs supplied by a private collector. The result of this is not only the worn “beached” appearance of many of the shells, but also an array of backgrounds and visible mounting media (from sticky tape on p. 27 to mounting putty on p. 61). The arrangement of the marine gastropod plates is haphazard, negating the original attempt to have text and figures logically and compactly arranged. Shell orientation is random, forcing the reader to rotate the book in various directions. The colored thumb guide, which allows quick location of the nonmarine mollusks at the family level (as German common names), is replaced in the marine section by the not very helpful arrangement at the class level (marine snails, marine bivalves). When compared to the excellent nonmarine part, it is odd to discover that readers interested in marine species are not “burdened” with minor details such as author and date references or figure scales.

Alfred Limbrunner deserves credit for many of the photographs of living nonmarine animals and all of the nonmarine shells. Unfortunately, authors and editor chose a problematic way to show their appreciation. On page 276 (not “275” as stated on p. 158), one finds a description of a new subspecies of Clausiliidae in his honor. In addition to inherent problems of introducing new names in commercial book publications, this case is even more complicated. The author of this new subspecies is not one of the book authors, but Hartmut Nordsieck, who (according to Steinbach’s introduction) assisted Falkner with the taxonomy of the volume, especially that of the Clausiliidae. This means that a proper citation for this new taxon must be the cumbersome “*Carinigera schuetti limbrunneri* H. Nordsieck in Fechter & Falkner in Steinbach, 1990.” The exact date of publication cannot be found in the book (the title verso just states “1990”), and has to be deduced from external sources: the advertisement flyer of the publishing company announced a delivery date of September 1990, the review copy was mailed on 17 October 1990.

Despite these points of critique, this book (more precisely, Falkner’s part of this book) is of exceptional quality and sets new standards for a malacological field guide. It is highly recommended for anybody interested in European mollusks.

Rüdiger Bieler

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

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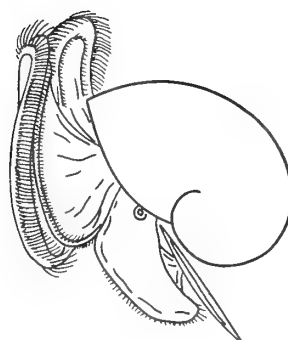
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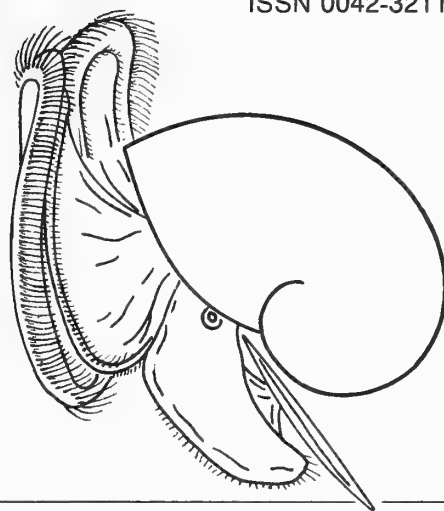
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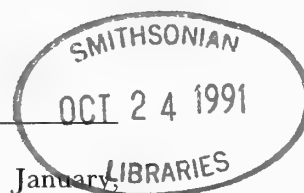
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Scope of the journal

The Veliger is open to original papers pertaining to any problem concerned with mollusks.

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Very short papers, generally not exceeding 500 words, will be published in a column entitled "NOTES, INFORMATION & NEWS"; in this column will also appear notices of meetings, as well as news items that are deemed of interest to our subscribers in general.

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A Bibliography and Brief Biography of G. Alan Solem, 1931-1990

by

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G. Alan Solem was born on 21 July 1931, in Chicago, Illinois, the son of a physician and a mother who was active in church work. The family lived in Oak Park, a suburb of Chicago. His association with the Field Museum of Natural History began in 1946, when he began work as a volunteer in the Division of Insects. By 1949, he was working with Dr. Carl P. Schmidt, Chief Curator of Zoology, and Dr. Fritz Haas, Curator of the Division of Lower Invertebrates.

He attended Haverford College, Haverford, Pennsylvania, obtaining his B.S., *magna cum laude*, in 1952. He did his graduate study at the University of Michigan, Ann Arbor, obtaining his M.A. in 1954 and his Ph.D. in 1956. At Michigan his mentor was Professor Henry Van der Schalie, and he worked during the summers at the Academy of Natural Sciences, Philadelphia, with Dr. Henry Pilsbry, as well as at the Field Museum with Dr. Haas.

In 1956 he joined the scientific staff of the Field Museum as the Assistant Curator of Lower Invertebrates, succeeding Dr. Haas as Curator in 1959, and becoming Curator of Invertebrates when the name of the Division was changed in 1971. He was still in that position at the time of his death.

Beginning in 1971, he was Lecturer for the Committee on Evolutionary Biology at the University of Chicago, where he also taught graduate seminar courses. From 1967 to 1975 he taught both undergraduate and graduate courses at Northwestern University, and directed the research of graduate students at both Chicago and Northwestern. He was appointed a Research Associate in the Department of Biological Sciences at Northwestern in 1970, and at the Australian Museum in 1976. He taught an adult education class in the operation and use of the scanning electron microscope at the Field Museum, 1978-1982.

He served as Vice President, President, and Past President of the American Malacological Union, as well as a Member or Chairman of many committees of that organization. He was a Counselor, Panel Member, Committee Chairman, or Chairman of four other professional soci-

eties, and was on the editorial boards of six scientific publications. He was a Member, Fellow, or Life Member of 10 scholarly scientific societies in four countries, and was named an Honorary Life Member of the Malacological Society of Australia.

He participated in 23 international congresses and meetings, presenting papers at nearly all of them. At 11 of the meetings, he was a symposium organizer and/or invited speaker.

In his 33 years at the Field Museum, he made 19 field trips, many including more than one country. In addition to two trips within the United States, he went once each to Panama, the Lesser Antilles, and Namibia, and three times to New Zealand and various small Pacific islands. However, the bulk of his field work was carried out in Australia, to which he journeyed 11 times. In all, he was out in the field for 40 months: three and a third years, 10% of his time at the Field Museum.

I began working for Dr. Solem as a volunteer in 1963, and continued as volunteer, student, and, finally, colleague over the next 27 years. With his encouragement I entered graduate school, and he was one of my teachers, a member of my doctoral committee, and the director of my research. I found him to be a perfectionist, insisting that everyone who worked for him put forth his or her very best, as he always did himself. He was a leader, rather than a driver: he never asked anyone to do anything that he was not willing and able to do himself. If a student was in difficulties, he could be patience personified, explaining the problem over and over again—if the student was really trying to understand. If he thought the student was just being lazy, he could be very brusque, and those who attempted to get by with second-rate work got very short shrift indeed.

Writing of the results of Dr. Solem's Australian field work, Victoria Huff, former collection manager in the Division of Invertebrates, says in a memo (1990) to Field Museum administration, quoted in a personal communication to me:

As a result of Dr. Solem's vigorous research activities and the enthusiasm that he generated among field associates and colleagues in Australia, Field Museum has built an impressive collection of Australian land snails. These collections include over 8,000 lots of land snails, many preserved in alcohol and suitable for further anatomical studies, virtually all with extremely precise locality data. Associated data include: shell measurements of many lots; over 5,500 SEM photographs of shells, jaws, and radulae; hundreds of detailed scientific illustrations of anatomy and shells; well over 300 computer-generated distribution maps; and a limited amount of frozen tissue samples, suitable for at least preliminary electrophoretic studies.

A colleague, Dr. Rupert L. Wenzel, Curator Emeritus of Insects, has written an excellent summary of Dr. Solem's work:

Solem's field work and research dealt with molluscs of many parts of the world, but his most important work focused on snails of the Pacific islands and the Australian Region. . . . He became interested in the problem of how numerous closely related species, presumably from a single or only a few colonizations, could evolve on one small island, possibly as a result of conditioning to specific food resources and microniches, leading in turn to microgeographic and reproductive isolation, followed by differentiation into species that differed in their feeding specializations.

This 'flowering' of species was exemplified by the endodontid snails . . . on the tiny Pacific island of Rapa, and appeared at variance with accepted biogeographic theory on island colonization and establishment of biotic equilibrium. It also conflicted with the then widely accepted doctrine . . . that new species did not form in the absence of (macro) geographic isolation. Solem's concern with these problems led him to pursue detailed analyses of differences in the feeding mechanism of snails, correlating them with differences in reproductive anatomy and niche and food specialization. These analyses are essential to delineating their evolutionary relationships and to exploring the history of their distribution through geologic time. . . .

[He was interested in Australian snails because] it was evident that they represented a largely unknown fauna and seemed to pose questions similar to those encountered in his studies of island faunas. In some ways they proved to be even more interesting because isolated 'islands' of vegetation possessed clusters of species that could interact for feeding and reproduction only during the scarce and very short periods of rain. Between rains, they underwent long periods of dormancy. . . . Additional field trips . . . added much more material and raised additional questions concerning the evolution and relationships of the [Australian] snail fauna to that of the rest of the world. (WENZEL, 1990)

Alan Solem was an extraordinarily productive writer. In addition to 45 popular articles and a children's book, he published 150 scientific papers, including encyclopedia articles, chapters for textbooks, and one semitechnical book. Two more papers were published after his death in 1990, and he left five completed family accounts to appear in *Fauna of Australia*, as well as 11 other scientific papers in press or submitted. Evaluating Dr. Solem's productivity, Dr. Wenzel writes:

[Solem's publications] set new high standards for the study and description of molluscs as well as for analysis of the data. . . . He described dozens of new genera and several hundred new species and subspecies, a remarkable output, but in itself not as important as the generalizations as well as other research which they make possible. (WENZEL, 1990)

As an editor and teacher of scientific writing, he held his students to his own high standards. Multiple rewrites were sometimes required before he was satisfied, but his students understood that he would never allow them to write themselves into indefensible corners. If a paper left the Museum with the Solem *imprimatur*, its acceptance for publication was assured.

Dr. Solem's most recent scientific illustrator, Mrs. Linnea Lahlum, who worked for and with him for 10 and a half years, spoke at his memorial gathering. A copy of her remarks was given to me, and among them were the following:

He was straightforward. He did not pretend. . . . He was extremely generous and considerate . . . always ready to listen and give what support he could. As busy as he was, he was never too preoccupied to care. . . .

He had a drive for achievement that was unusual. The atmosphere of productive activity that he established was infectious. . . . He was demanding, but he made you feel that he had perfect faith in your ability to meet the demand. He had the quality of inspiring excellence. . . . [He was] genuinely appreciative of the work you did [and] never took your work or its quality for granted. . . . He had his own standard of excellence he was always testing himself against, and he knew that we, too, had our own standards, and must be encouraged to surpass them.

. . . Working with [him] was never boring. He *made* it interesting. There was a sense of an adventure in progress. He took such enjoyment in it, such relish of the discovery of the new. [He] once wrote, "The joy of scientific research. Partly answer one question, reveal a dozen others. Learn a bit, question a lot. Improve the quality of the questions asked. A continuous and enjoyable process on which I'm well along." (SOLEM, 1981).

He was a grantsman extraordinaire. Between 1961 and 1988, he was awarded 15 grants totaling \$771,000, with additional funding from private individuals. One of his

grants, from the National Science Foundation, enabled the Field Museum to acquire its first electron microscope. Thanks to his high professional standing and persuasiveness, at least three major mollusk collections were given to the museum. The Hubricht Collection of eastern North American land snails, comprising 500,000 specimens in 48,000 lots, had been promised to the Museum before Dr. Solem's death, and arrived shortly thereafter. He had been looking forward eagerly to its coming, because he said it would make the Field Museum's holdings "the finest land snail collection anywhere."

He died on 26 February 1990, leaving a wife, Sylvia, and two adult children, Anders and Kirsten. He is also survived by his sister, Elizabeth (Mrs. George) Dutton. He is most sorely missed, both personally and professionally, by all who knew, or knew of, the man and his work.

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Note: At the time of Dr. Solem's death, six of his scientific papers were in press, 11 had been submitted for publication, and one was in review. The paper in review and one of those in press were published after his death, and appear above (1990). When all of the remaining papers have been published, an addendum to this bibliography will appear. A list of his new molluscan taxa will also appear at a later date.

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Growth, Size at Sexual Maturity, and Egg-Per-Recruit Analysis of the Abalone *Haliotis fulgens* in Baja California

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Abstract. The growth rate and size at sexual maturity of *Haliotis fulgens* were measured at Bahía Tortugas, Baja California Sur. The parameters of the fitted von Bertalanffy growth equation were: $K = 0.38$, $L_{\infty} = 183$ mm. There was no significant difference in growth rate between the sexes. The length at which 50% of a sample reached sexual maturity was 105 mm. These data, with other published data on *H. fulgens*, were used to do yield-per-recruit and egg-per-recruit analyses. Maximum yields occurred at ages 4–7 years, according to the natural mortality rate chosen. At the current fishery size limit (145 mm), egg production levels are 6–17% and are considered to be dangerously low and inadequate to maintain recruitment.

INTRODUCTION

Numerous abalone fisheries around the world have collapsed with increasing fishing pressure, and in some cases this has been attributed to the removal of too much of the parent stock (recruitment overfishing) (reviewed by BREEN, in press). In consequence, simple egg-per-recruit models have been devised to show the number of eggs produced under different fishing intensities and with different size limits (SLUCZANOWSKI, 1984, 1986; BREEN, in press; TEGNER *et al.*, 1989). Such models can be used in a population at equilibrium to specify size limits to maintain a

given level of egg production or, alternatively, to examine a fishery in retrospect to see what egg production level maintained the stock or, in the case of a collapsed fishery, led to such a collapse. In the absence of knowledge of the relation between breeding stock size and recruitment, egg-per-recruit analyses of many stocks, including collapsed ones, can give clues as to appropriate egg production levels.

The abalone *Haliotis fulgens* Philippi is taken commercially in Baja California where it comprises up to 85% of the abalone catch (TURRUBIATES *et al.*, 1987), but little is known of the parameters required to apply an egg-per-recruit model to the fishery. In this paper we describe an

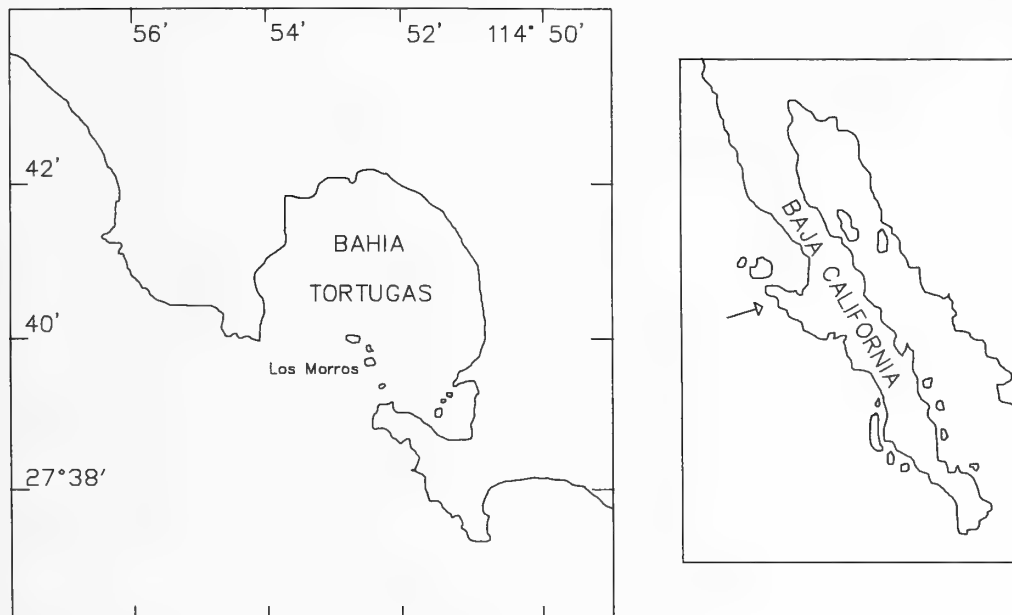


Figure 1

Map of Bahía Tortugas showing Los Morros Islands, and (on right) their location in Baja California.

experiment to measure the growth rate of *H. fulgens* at Bahía Tortugas, Baja California (Figure 1). We also attempted to measure the natural mortality rate, M , but the experiment failed, and we discuss it only to illustrate the problems of dealing with a cryptic species. We determined size at sexual maturity, and used these results and other published information to do yield and egg-per-recruit analyses for *H. fulgens*. We then apply the results to management of the fishery and suggest an appropriate size limit.

MATERIALS AND METHODS

By agreement with the local fishermen's cooperative, a study site on the inner shore of Los Morros Island was selected and closed to fishing. The shore here is composed of large boulders and blocks up to 2 m diameter close to shore and a deeply creviced reef of 1–2 m relief. The giant kelp, *Macrocystis pyrifera*, forms a dense forest to about 2 m depth and, beyond the forest, the seagrass *Phyllospadix torreyi*, coralline algae, and other red and brown algae dominate exposed rock surfaces to about 5 m depth where rock is buried by sand. *Haliotis fulgens* mainly occurred at the edge of the *Macrocystis* forest from 2 to 4 m depth.

Individuals of *Haliotis fulgens* between 70 and 140 mm shell length (SL) were measured and marked with plastic numbered tags riveted to the shell through the proximal pore-hole (PRINCE, 1991) in August 1987, November 1987, and May 1988, and placed within an area marked out with chain. In August 1988, one year after the initial tagging, the area was thoroughly searched for 35 hr diving time and marked individuals recaptured. Subsequent further searching for 9 hr increased the number of recaptures.

The abalone taken in August 1987 were sexed, by visual inspection of the gonad, prior to marking, and the data obtained were used to determine size at sexual maturity. In this species the gametes are mature from June to September and the sexes are readily distinguishable visually by color (GUZMÁN DEL PRÓO, in press); visual inspection is considered to give a reliable indication of the presence of gametes, but not the onset of spawning.

Growth rates were estimated by fitting von Bertalanffy growth curves to growth increment data by the method of FABENS (1965). For this calculation we excluded growth data where the period at liberty was less than a year, in order to avoid bias from differential seasonal growth.

A simple model was developed to examine the biomass yield (BEVERTON & HOLT, 1957) and production of eggs (SLUCZANOWSKI, 1984) during the life of a cohort. We used the following equations as inputs. In the absence of published fecundity estimates for *Haliotis fulgens* in Baja California we used: a mean fecundity (F) of 2.67 million eggs at 172 mm length, derived from TUTSCHULTE (1976) and TUTSCHULTE & CONNELL (1988) for *H. fulgens* at Santa Catalina; a length-weight relationship of $W = 2.72 \times 10^{-5} L^{3.43}$ (after GUZMÁN DEL PRÓO, in press); and a mean length at sexual maturity of 105 mm (this paper). We assumed fecundity was linear with total weight (W) and derived the equation:

$$F = 0.0026W - 0.61.$$

In these equations W is expressed in g, L in mm, and F in millions of eggs.

Parameters of the von Bertalanffy growth equation are those given for females in this paper.

Table 1

Values of the parameters of the von Bertalanffy growth equation for *Haliotis fulgens* at Los Morros. The total number (32) includes 4 that were sexually immature.

Sex	n	K (yr ⁻¹)	SE	L _∞ (mm)	SE
Male	15	0.39	0.10	181.2	8.3
Female	13	0.41	0.09	179.9	8.1
Total	32	0.38	0.04	183.1	6.1

RESULTS

Growth and Size at Maturity

Annual increment data for mark-recapture data are plotted in Figure 2 and estimates of the parameters of the von Bertalanffy growth equation are given in Table 1 for males, females, and all data, which includes juveniles. The slight differences in growth rate between the sexes are not significant. We did not have data on the growth rate of *Haliotis fulgens* below about 80 mm in this study. However, TURRUBIATES (1989) found that the growth rate of juveniles was 35 mm per year for the first 2 years at a different site in Bahía Tortugas. Assuming that the mean length of *H. fulgens* is 70 mm at 2 years, a mean growth curve can be constructed for the Los Morros site (Figure 3).

A plot of the percent sexually mature individuals against size (Figure 4) shows that sexual maturity occurs between 70 and 140 mm SL. Fifty percent are sexually mature at about 105 mm SL, suggesting that sexual maturity is attained at about 3 years of age.

The sex ratio changes from 1:2 (males to females) for

those <120 mm SL to 1.17:1 for those >120 mm SL. The change in sex ratio with size is significant (Cochrans Test: $\chi^2 = 4.07$; $P < 0.05$) and unless differential mortality occurs, suggests a slightly faster growth rate of males than females because of the higher proportion of mature females in smaller size classes.

Emigration from the study site was about 12% of those recaptured. Four individuals were found during extensive searching for 50 m beyond the marked boundary. The mean distance moved by these abalone was about 14 m (maximum 25 m) in a year, in each case in the direction of the approaching swell. In addition, fishermen reported three more tagged abalone that were estimated to have moved about 50 m.

Egg-Per-Recruit and Yield-Per-Recruit Analysis

Egg-per-recruit analysis and biomass yield (Figure 5) are presented as a percentage of the maximum number of eggs produced by a cohort, or the maximum weight of the cohort, as the case is, for three rates of M —0.1, 0.2, and 0.3—for a range of ages at first capture.

We chose a high, fixed value of F for the analysis because this is the most realistic assumption of the intensity of fishing during the recent history of the fishery (see Discussion). It is also more useful for management because, in the future, control of fishing is likely to be more easily achieved by an output control, such as a size limit, than an input control, such as a direct control of effort.

The results show that egg production increases more or less monotonically from ages 5 to 10 years for the three chosen values of M , whereas biomass decreases from maxima at 4–8 years according to the value of M .

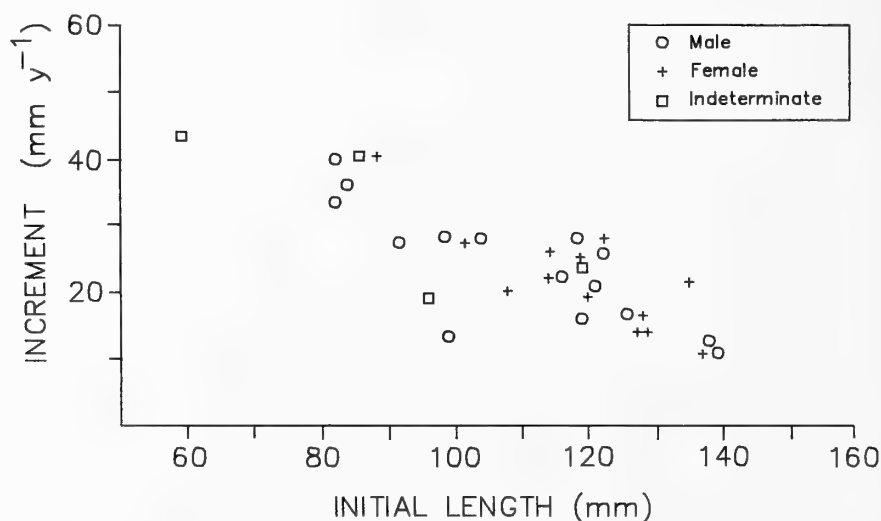


Figure 2

Plot of annual increment data for *Haliotis fulgens* at Los Morros for males, females, and those of indeterminate sex.

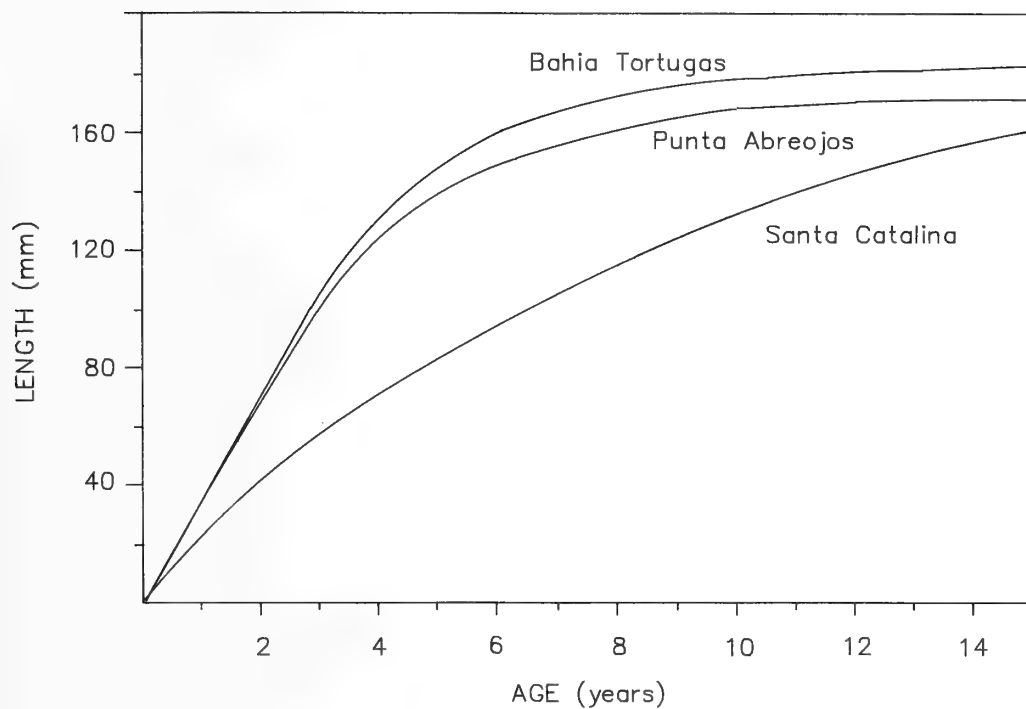


Figure 3

Growth curves of *Haliotis fulgens* at Los Morros (Bahía Tortugas) (this study), Punta Abreojos (GUZMÁN DEL PRÓO & MARIN, 1976), and Santa Catalina, California (TUTSCHULTE & CONNELL, 1988).

DISCUSSION

Growth, Size at Maturity, Sex Ratio, and Mortality

Previously published growth rates of *Haliotis fulgens* are given in Table 2 (see review by DAY & FLEMING, in press) and compared graphically in Figure 3. The growth rates of *H. fulgens* are almost identical at Punta Abreojos and Los Morros, and both are much faster, especially at smaller sizes, than that recorded by TUTSCHULTE & CONNELL (1988) at Santa Catalina Island. This is consistent with GUZMÁN DEL PRÓO's (1989) statement that the growth rate of abalone decreases with increasing latitude along the Californian peninsula. Compared with the growth rates of other abalone species (DAY & FLEMING, in press) this species in central Baja California must rank among the fastest growing abalone in the world.

The size at sexual maturity from our data occurs over a wide size range (70–140 mm), an only slightly greater range than that given by TUTSCHULTE & CONNELL (1981), 61–128 mm, although these authors suggested a much slower rate of growth. Our values are also less than that given by GUZMÁN DEL PRÓO (in press) in his review of earlier work; 50% of the population was mature at 141 mm SL. Size at sexual maturity has been suggested to be age-dependent rather than size-dependent (PRINCE, 1989), and this accords with our experience (SHEPHERD & LAWS,

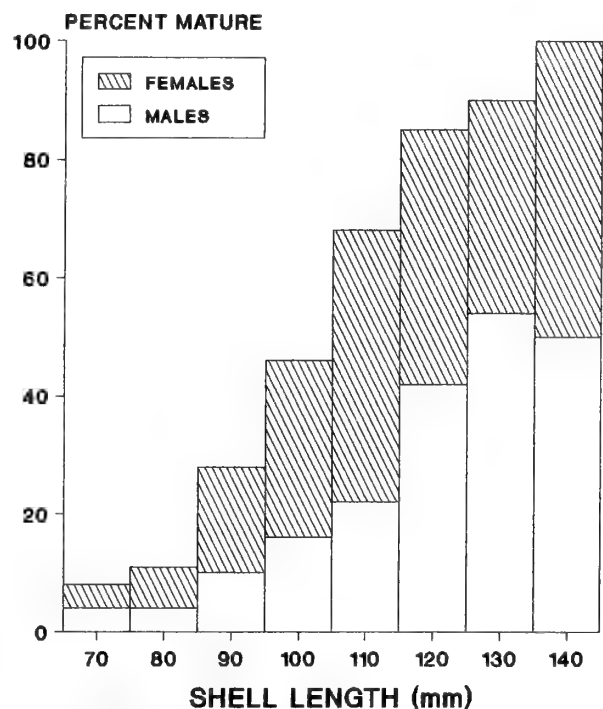


Figure 4

Percentage of sexually mature *Haliotis fulgens* with size.

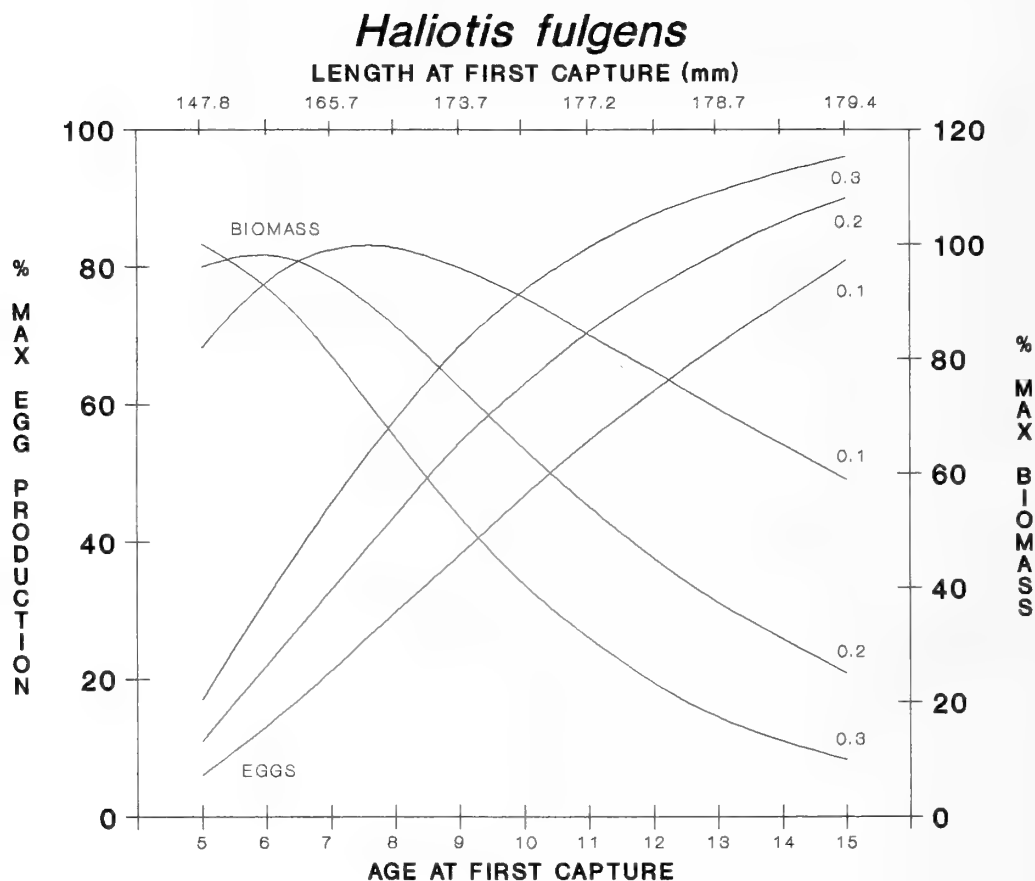


Figure 5

Yield-per-recruit and egg-per-recruit curves for *Haliotis fulgens* at M values of 0.1, 0.2, and 0.3, for high values of $F(= 8)$.

1974; GUZMÁN DEL PRÓO, in press). Because growth rates can vary greatly between reefs, the size at sexual maturity would also be expected to be variable between sites.

The significance of a changing sex ratio with size is still not clear (see TUTSCHULTE & CONNELL, 1981). SHEPHERD & HEARN (1983) suggested that differential growth between the sexes was the most likely cause of changing sex ratios. This implies that allocation strategies may vary between the sexes in a population, a possibility that deserves further study.

Our tagging experiment was conducted in a way that allowed for measurement of the natural mortality rate (M)

by the BEINSEN & POWELL (1979) method. However, of the 533 marked abalone released only 10% were recaptured; the obtained value of M' (0.31) did not differ significantly from zero, and is of no value. The experiment illustrates the problems encountered when the recapture rate is low. The low recapture rate was due partly to the cryptic nature of *Haliotis fulgens* in a deeply creviced habitat that contained many large boulders that could not be overturned, partly to the abundance of *Phyllospadix* and algae which made searching difficult, and partly to low visibility due to red tide. A low searching efficiency is not inconsistent with a high value of F ; the former applies to

Table 2

Parameters of the von Bertalanffy growth equation for *Haliotis fulgens* at different sites.

Place	Latitude	K (yr^{-1})	L_{∞} (mm)	Sex	Authority
Santa Catalina	37°N	0.10	205	both	TUTSCHULTE & CONNELL (1988)
Punta Abreojos	26°40'N	0.38	171	male	GUZMÁN DEL PRÓO & MARIN (1976)
Punta Abreojos	26°40'N	0.37	170	female	GUZMÁN DEL PRÓO & MARIN (1976)

the smaller, cryptic fraction of the population whereas the latter applies to the larger, more exposed fraction. Further, the study site may have contained more cryptic habitat than is typical of fished habitats. The problem of low searching efficiency was experienced by SHEPHERD *et al.* (1982) in measuring M for *H. rubra*, a species of similar cryptic habit. SHEPHERD & BREEN (in press) have discussed the problem and recommended a pilot experiment to obtain some idea of the likely movement and recapture rate.

Estimates of M for *Haliotis fulgens* range from 0.07 to 0.53 (reviewed by SHEPHERD & BREEN, in press) but we think the high values are not realistic for adult abalone. For the purpose of the egg-per-recruit analysis we use M values of 0.1–0.3, which should span the likely range of M .

Implications for Management

The history of the Mexican abalone fishery in Baja California is described by GUZMÁN DEL PRÓO (in press), and salient features are summarized here. From the early 1960s the fishery was subject to high fishing pressure. From 1970 to 1985 the combined annual catch of *Haliotis fulgens* and *H. corrugata* in Zones II–IV (the mid-Baja California coast that includes Bahía Tortugas) declined to one-fifth, although the proportion of *H. fulgens* increased, indicating a proportionally smaller decline of that species. The density of *H. fulgens* apparently declined to one-third in the same period (GUZMÁN DEL PRÓO, in press). It seems reasonable to assume that the fishing mortality rate (F) was high (>1.0) during this period.

Size limits existed in name only until 1984, when a limit of 145 mm SL was enforced by requiring divers to land abalone in the shell. However, *Haliotis fulgens* has a cryptic habitat to at least 140 mm SL (TUTSCHULTE, 1976, unpublished), so that, even under intense fishing, few individuals <130 –140 mm SL would have been taken. We conservatively assume that the age of first capture is 5 years (=148 mm SL).

On the basis of the above assumptions, egg production since 1970 would have been in the range of 6 to 17% of the maximum possible according to the chosen value of M . Intuitively, this seems extremely low, and raises the possibility that recruitment overfishing (reduction of parent stock to a level that adversely affects recruitment) may have occurred, and precipitated the decline in catch and density during the history of the fishery (GUZMÁN DEL PRÓO, in press). NASH (in press) presented evidence suggesting that at least 50% of the egg production potential should be maintained in an exploited stock. SLUCZANOWSKI (1984, 1986) suggested minimum levels of 40%. SHEPHERD (1991) found that recruitment failed in an isolated population, when the population density declined to around 32% of the virgin population and when the fraction of the population that aggregated for spawning fell to 6%. However, such values are at best suggestions only until the stock-recruitment relations in abalone are better known.

Until more information on natural mortality is available, it would be prudent to increase the size limit to around 165 mm SL to ensure 20–40% egg production. This measure would be certain to have serious social and economic implications, which would need to be explored.

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Growth Rings Within the Statolith Microstructure of the Giant Squid *Architeuthis*

by

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Abstract. The microstructure of a statolith taken from a juvenile, female specimen of giant squid *Architeuthis* sp. (42.2 cm ML) trawled off southern Australia was examined. The statolith was mounted in thermoplastic cement and ground and polished on both the anterior and posterior surfaces to reveal the growth rings from the nuclear region to the edge. The growth rings were similar in appearance to daily growth rings observed in other oegopsid and myopsid squids. Based on replicate ring counts, the *Architeuthis* specimen was 153 days old and had an average daily growth rate of 2.76 mm per day. The presence of growth rings within the statoliths of the giant squid indicates that growth rings exist across the spectrum of cephalopod size from the smallest species, *Idiosepius*, to the largest of all cephalopods, *Architeuthis*.

INTRODUCTION

Growth rings have been observed in the statoliths of many cephalopod species: in the oegopsid squids *Illex illecebrosus* (HURLEY & BECK, 1979), *Illex argentinus* (RODHOUSE & HATFIELD, 1990), *Todarodes sagittatus* (ROSENBERG *et al.*, 1981), and *Gonatus fabricii* (KRISTENSEN, 1980); in the myopsid squids *Alloteuthis subulata* (LIPINSKI, 1986), *Photololigo edulis* (NATSUKARI *et al.*, 1988), *Heterololigo bleekeri* (KINOSHITA, 1989), *Sepioteuthis lessoniana* (JACKSON, 1990a), *Loliolus noctiluca* (JACKSON, 1990b), *Loligo forbesi* (MARTINS, 1982), *Loligo opalescens* (SPRATT, 1978), *Loligo gahi* (RODHOUSE & HATFIELD, 1990), and *Loligo chinensis* (JACKSON, 1990b). Growth rings have been shown to exist also in the sepoids *Rossia glaucopis* (KRISTENSEN, 1980) and *Idiosepius pygmaeus* (JACKSON, 1989). Here we report

on the statolith ring structure of a juvenile giant squid (*Architeuthis* sp.) that was trawled off the southern coast of Australia.

MATERIALS AND METHODS

The specimen of *Architeuthis* sp. (a female, 42.2 cm ML) was captured on 30 January 1982 on a cruise of the CSIRO FRV *Soela* using an International Young Gadoid Pelagic Trawl (IYGPT). The tow was taken off New South Wales Australia (33°44'S, 153°00'E) between 1845 and 1950 hr, obliquely from the surface to a depth of 600 m. Bottom depth at the locality was approximately 2000 m. Details of the specimen will be published elsewhere (Lu and Dunning, unpublished). The statoliths were removed before preservation of the specimen, placed in 70% ethanol, and

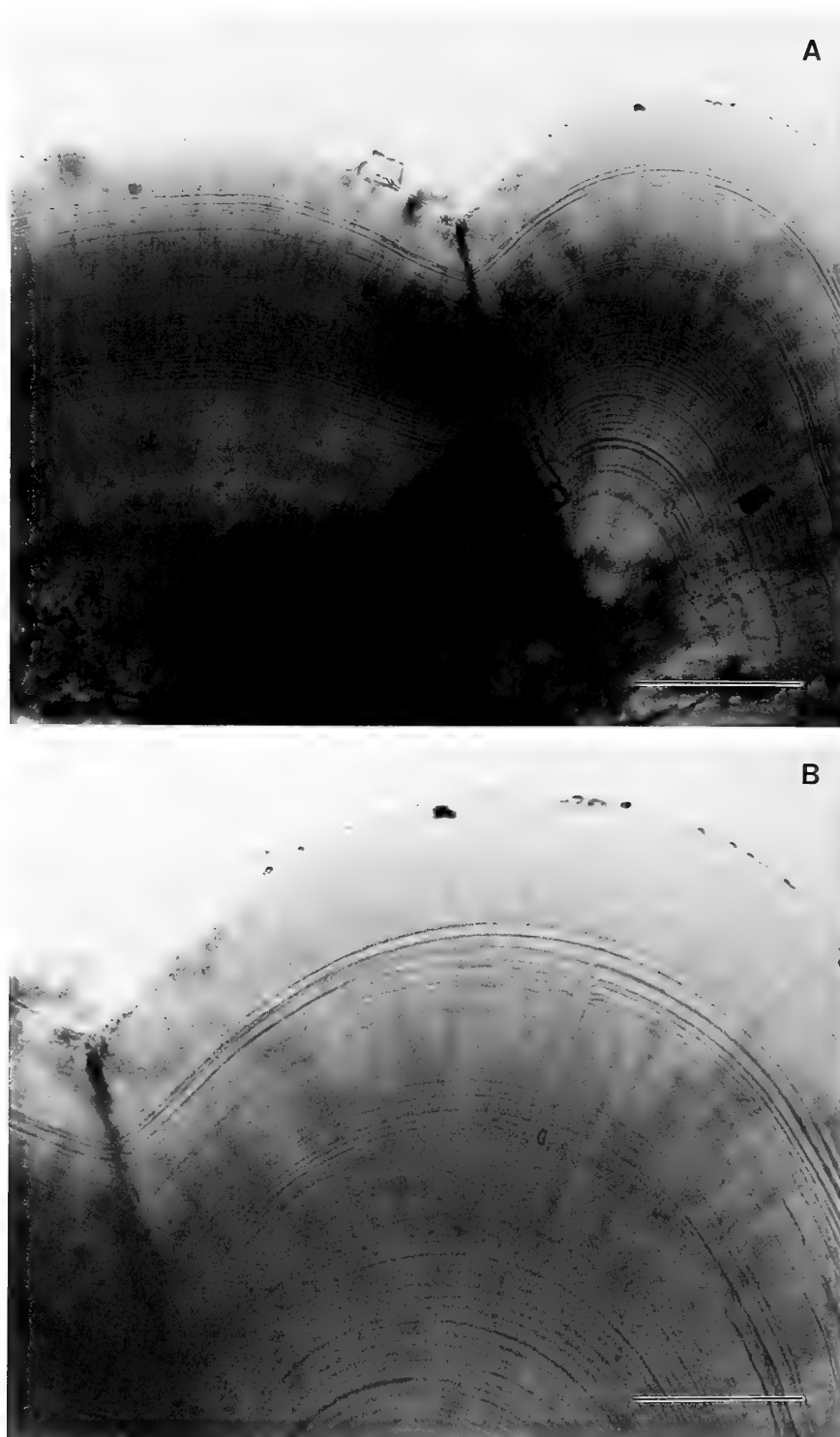


Figure 1

Growth rings within the statolith microstructure of a juvenile *Architeuthis* sp. A. Dorsal dome region of statolith; scale bar = 80 μm . B. Close-up of ring structure within the dorsal dome showing clear ring sequence to the statolith margin; note the unusual discontinuity within the ring structure approximately 17 rings in from the margin; scale bar = 40 μm .

subsequently examined in January 1990. The years of preservation in ethanol did not appear to damage the statoliths.

One of the statoliths was embedded in the thermoplastic cement Crystal Bond®. The ring structure on the edge of the dorsal dome region was visible immediately upon being embedded in the cement. However, the statolith required both grinding and polishing on both the anterior and posterior surfaces to produce a thin section and to reveal the rings deeper within the microstructure. Grinding and polishing techniques were the same as previously described (JACKSON, 1990a, b).

RESULTS AND DISCUSSION

Specimen Identification

The specimen of this study was identified as *Architeuthis* sp. on the basis of several distinguishing features: it possessed a straight simple funnel-locking cartilage, the buccal connectives were attached to the dorsal border of arm IV, and the tentacular club had four rows of suckers, with those on the medial rows of the manus much larger and those on the marginal rows small. Also, a distinct cluster of numerous small suckers and knobs were at the proximal end of the manus, and two longitudinal rows of alternating suckers and pads were on the tentacular stalks. The specimen is lodged at The Museum of Victoria (registration number: F57913).

Statolith Analysis

The grinding and polishing of the *Architeuthis* statolith produced a translucent section in which the microstructural ring sequence was visible (Figure 1A) with ring definition very clear to the outer edge of the dorsal dome (Figure 1B). Although the ring sequence could be traced back to the nuclear region, no clear point marking the start of the ring sequence could be seen. Examination of more statoliths will be needed to define accurately the nuclear region. The growth rings were similar in structure to growth rings observed in loliginids, for example by NATSUKARI *et al.* (1988) and JACKSON (1990a, b), and in other oceanic squids, for example by KRISTENSEN (1980), ROSENBERG *et al.* (1981), and RODHOUSE & HATFIELD (1990). The ring structure was bipartite and consisted of a narrow dark zone and a broader light (more translucent) zone. Three replicate counts of all the growth rings from the nuclear region to the edge were very close (154, 154, 150).

Architeuthis represents the upper end of the size range of cephalopods, with individuals reaching huge dimensions of over 20 m total length and a mantle length of 6 m (ROPER *et al.*, 1984). However, biological data for this species are fragmentary and mostly derived from the examination of a relatively few stranded specimens (CLARKE, 1966; ROPER & BOSS, 1982; BOYLE, 1986).

Although it would be difficult to validate the periodicity of the growth rings within the *Architeuthis* statoliths, the

rings do resemble growth rings that have been shown to be laid down daily in other species. Assuming the daily formation of growth rings and a mantle length at hatching of approximately 1 mm, the specimen examined would have been about 153 days old with an average growth rate of 2.76 mm per day.

Obtaining statolith age estimates from a number of different-sized individuals of *Architeuthis* would allow a more accurate determination of the form of the growth curve for this squid.

Statolith growth ring analysis has now spanned the entire size range in cephalopods, from the tiny *Idiosepius* (<2 cm ML) (JACKSON, 1989) to this specimen of giant squid, *Architeuthis* (42.2 cm ML). The maximum size of *Architeuthis* indicates that statolith rings are laid down in cephalopods over a size range of over three orders of magnitude. Future research on the aging of oceanic squids promises to provide insights into the growth dynamics of many other poorly understood species.

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Seasonal Variation in Biochemical Composition of Three Size Classes of the Chilean Scallop *Argopecten purpuratus* Lamarck, 1819

by

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Abstract. Seasonal changes in protein, carbohydrate, and lipid levels of different size classes of the Chilean scallop *Argopecten purpuratus* Lamarck, 1819, were examined in order to describe these changes, both as a function of reproductive activity and age. Three size classes of individuals were examined: 20, 50, and 80 mm mean length. Separate analyses were made for adductor muscle, mantle, and gonad body components. Protein was always the most abundant substrate in all components. Adductor muscle protein content exhibited a different seasonal pattern for each size class of animals. Adductor muscle lipid levels varied significantly only in the middle size class, and the carbohydrate content showed a similar seasonal course for all size classes. The gonad had the greatest variation in biochemical composition, not only seasonally, but also with size class. A negative correlation between gonad index and carbohydrate content of all examined components was observed in summer for 80-mm scallops, indicating that, in *A. purpuratus*, this metabolic substrate is being utilized for the maturation of gametes. In ripe gonads, lipid and protein levels of the female portion were higher than those of the male portion, indicating that these substrates become the constituent and reserve materials for larvae. Biochemical analyses of the mantle revealed clear differences among the three size classes of individuals, suggesting that this tissue could be a site for storage of metabolic substrates to be utilized for growth rather than for gametogenesis.

INTRODUCTION

The scallop *Argopecten purpuratus* Lamarck is one of the most commercially important bivalves in northern Chile. After being intensively fished for several years, its culture under managed conditions has been developed. DISALVO *et al.* (1984) were the first to study the feasibility of rearing this scallop in mass culture and described the entire growth cycle from egg to the attainment of adult size. *Argopecten purpuratus* is a functional hermaphrodite and presents a continuous reproductive cycle with a major spawning peak in late summer and a minor one in autumn (BROWN & GUERRA, 1982; WOLFF, 1988).

Seasonal changes in the composition and utilization of metabolic substrates in marine bivalves have generally been attributed to reproductive activity (for reviews see GIESE, 1969; GABBOTT, 1976, 1983). However, the studies of Pectinidae have shown that the manner in which nutrient reserves are utilized for gametogenesis is variable. For *Pecten maximus* (FAVERIS, 1987), *Chlamys opercularis* (TAYLOR & VENN, 1979), and *Argopecten irradians con-*

centricus (BARBER & BLAKE, 1981), energy for the maturation of gametes comes from reserves of glycogen and protein stored in the adductor muscle. In *Argopecten irradians irradians*, gametogenesis occurs mainly at the expense of adductor muscle protein and lipid reserves (EPP *et al.*, 1988). The energy for this process in *Chlamys septemradiata* (ANSELL, 1974) comes mainly from ingested food, whereas in *Placopecten magellanicus* it comes from both stored reserves and ingested food (THOMPSON, 1977; ROBINSON *et al.*, 1981).

The present study investigates seasonal changes of the principal biochemical constituents of some tissues of *Argopecten purpuratus*. Individuals of different sizes are examined in an attempt to explain seasonal patterns, not only as a function of reproductive activity, but also as a function of age.

MATERIALS AND METHODS

The scallops *Argopecten purpuratus* were obtained from an experimental culture in Herradura Bay, Coquimbo, Chile

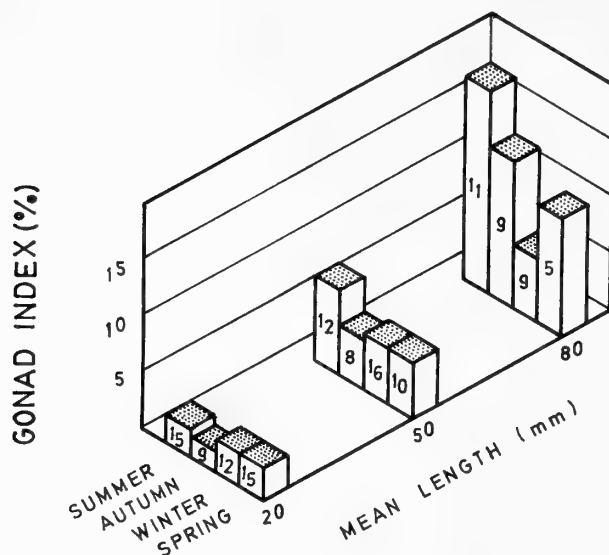


Figure 1

Seasonal changes in the gonad index of three size classes of *Argopecten purpuratus*. Number within columns is (n).

(30°S). Three size classes of animals were chosen: 15–25 mm, 45–55 mm, and 75–85 mm in shell length. I shall refer to them by their mean values: 20, 50, and 80 mm, respectively. Three times a week, 6 to 10 individuals of each size class were sampled for biochemical analyses. This sampling was done during the following periods: summer, from 15 December to 30 January; autumn, from 15 March to 30 April; winter, from 15 June to 30 July; and spring, from 15 September to 30 October.

Individuals were cleaned, blotted dry, and weighed with the shell and without it. Adductor muscle, gonad, and mantle body components were separated, weighed, and dried to constant weight at 70°C. When the gonads appeared ripe, male and female portions were easily distinguished and dissected separately. The male portion has a light creamy white color while the female is orange colored. Twenty milligrams of dried tissue was homogenized in 1 mL of deionized water and subsamples of this homogenate were used to determine protein, carbohydrate, and lipid levels ($\mu\text{g}/\text{mg}$ dry weight).

Proteins were assayed by the Lowry method (LOWRY *et al.*, 1951) using bovine serum albumin as the calibration standard. Carbohydrates were determined using the phenol-sulfuric acid method of DUBOIS *et al.* (1956) with minor modifications: one aliquot of the original homogenate was resuspended in 10% trichloroacetic acid, placed in a 65°C hot water bath for one hour, cooled, and centrifuged for 15 min at 6000 rpm. One milliliter of supernatant was taken and 2 mL of phenol reagent was added and mixed rapidly. Five milliliters of concentrated sulfuric acid was then added, mixed thoroughly, and heated in boiling water for 20 min. After cooling, optical density was read at 490

nm on a Shimadzu spectrophotometer using oyster glycogen as the standard. Lipids were extracted from 0.2 mL of the original homogenate with chloroform-methanol (2:1). Portions of this extract were used for colorimetric determination with phosphovanillin reagent, using cholesterol for calibration (BLIGH & DYER, 1959; POSTMA & STROES, 1968).

The gonad index, used as an indicator of reproductive activity, was determined as the percentage of the total tissue weight of the animal that consisted of gonad.

One-way and two-factor analyses of variance were used to test for differences in biochemical composition among seasons and size classes of individuals (STEEL & TORRIE, 1980). A Tukey's test was applied to evaluate the significance of the possible differences found (STEEL & TORRIE, 1980).

RESULTS—GONAD INDEX

The gonad index of *Argopecten purpuratus* exhibited a seasonal pattern that was different for each size class of individuals (Figure 1). The smallest class of *A. purpuratus* (20 mm) did not show significant changes in this index throughout the year. The other two classes (50 and 80 mm) showed the highest values in summer, which were coincident with visual estimation of a prespawning stage of maturity. Notwithstanding, in summer, 50-mm scallops showed a significantly lower index (Tukey's test, $P < 0.05$) than 80-mm individuals. After this, the gonad index declined steadily in the 80-mm scallops to a minimum value in winter, which began to recover towards spring. In 50-mm animals, the index fell to a minimum value in autumn.

RESULTS—BIOCHEMICAL COMPOSITION

Adductor Muscle Analyses

Protein: Of the three biochemical constituents analyzed, protein was always the most abundant (Figure 2A). This metabolic substrate exhibited seasonal variations that differed according to the mean length of individuals (Table 1). In the 20-mm group, protein content remained fairly constant in summer and autumn but was significantly greater ($P < 0.05$) in winter. In 50-mm scallops, a small rise was present in autumn, after which there was a significant decrease ($P < 0.05$) in winter and a rapid recovery in spring. In the 80-mm size class, protein content remained fairly constant all year except for a significantly higher value ($P < 0.05$) in spring (Appendix 1).

Carbohydrate: This substrate showed a clear seasonal pattern (Figure 2B), but two-factor analysis of variance indicated no variation of this pattern between size classes of scallops (Table 1). The carbohydrate levels in summer were rather low, increased in autumn, decreased (except in 20-mm animals) in winter, and then attained high values in spring. This last increase was as high as 363% in the largest individuals (Appendix 1).

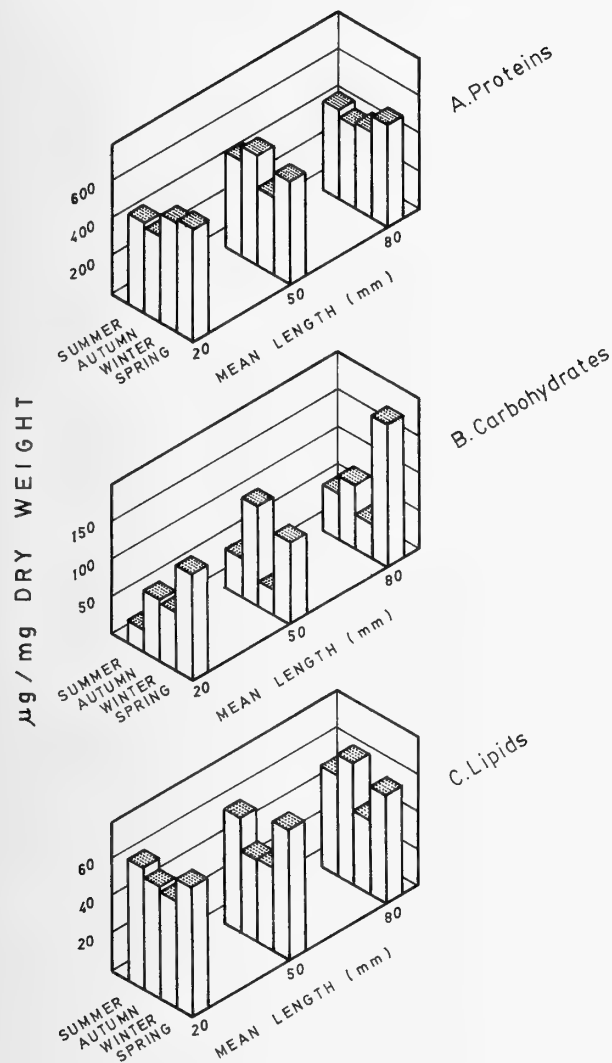


Figure 2

Seasonal changes in protein (A), carbohydrate (B), and lipid (C) contents of adductor muscle of three size classes of *Argopecten purpuratus*.

Lipids: Two-factor analysis of variance for this constituent showed that seasonal variation was independent of body size (Table 1). Nevertheless, statistical analyses of the differences (Tukey's test) showed that these were significant only for the 50-mm individuals. The lipid content of these animals decreased significantly in autumn (Appendix 1). This low value was sustained in winter and then underwent a great increase (63%) in spring (Figure 2C).

Gonad Analysis

This tissue showed the greatest variation in the content of its biochemical components, not only with respect to season, but also (with the exception of lipids) with respect to scallop sizes (Figure 3, Table 2; for actual values see Appendix 2).

Table 1

Two-factor analysis of variance for adductor muscle biochemical components of *Argopecten purpuratus*. Season and size are the main effects considered. ns, not significant; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

	d.f.	F
Proteins		
season	3	6.37***
size	2	8.12***
interaction	6	4.23**
residual	59	
Carbohydrates		
season	3	18.71***
size	2	0.74 ns
interaction	6	2.11 ns
residual	59	
Lipids		
season	3	5.24**
size	2	2.24 ns
interaction	6	1.17 ns
residual	56	

Proteins: As in adductor muscle, protein was the major organic constituent in the gonad. The smallest size class of animals exhibited the lowest value in summer, which thereafter increased steadily to a maximum in spring. The pattern of changes was exceptional in mid-length scallops; protein content was low in summer, increased 45% ($P < 0.05$) in autumn, then decreased significantly in winter, and again increased, 53% ($P < 0.05$), in spring. In the largest size class of animals, the summer value fell steadily towards the winter value when it amounted to only 61% of the summer level. After this, there was a rapid recovery in the spring. The winter value was statistically different from the values of the other three seasons. Comparisons within the same season show that, in summer, 80-mm-length scallops exhibited the highest protein level, whereas, during the rest of the year, 20- and 50-mm-length individuals had larger values (Figure 3A, Appendix 2).

Carbohydrate: The seasonal pattern for carbohydrate showed differences between size classes of animals (Figure 3B, Table 2). A significant increase ($P < 0.01$) in carbohydrate content occurred for all size classes during autumn after very low levels in summer. In 50-mm scallops this increase amounted to 239%. There was then a significant decrease ($P < 0.05$) in winter, followed by a small recovery in spring, which was significant only for 50-mm animals. The spring value for the largest scallops was 116% higher ($P < 0.05$) than the summer value.

Noteworthy differences in gonadal carbohydrate levels also occur between different size classes within the same season (Appendix 2). In summer and autumn, values for the biggest scallops are significantly less ($P < 0.05$) than

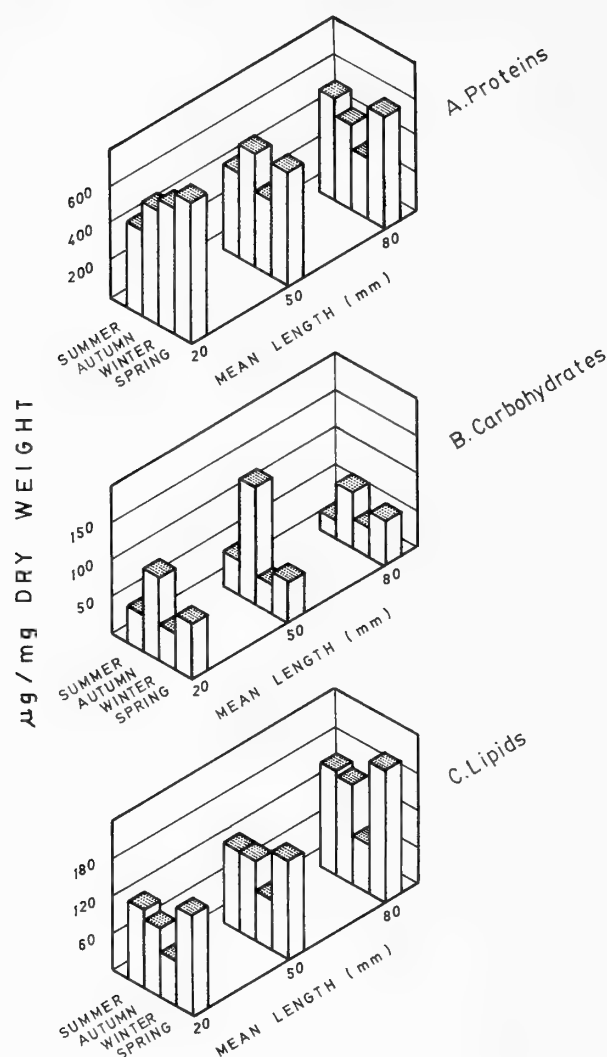


Figure 3

Seasonal changes in protein (A), carbohydrate (B), and lipid (C) contents of gonad tissue of three size classes of *Argopecten purpuratus*.

the corresponding values of the other two size classes of specimens.

The mean carbohydrate content of all body components examined was related to the gonad index (GI) during the summer and, for 80-mm scallops, there was a negative correlation between these two variables, described by the equation:

$$\ln \text{carbohydrate} = 4.57 - 0.097 \text{ GI}$$

$$r = -0.84 \quad r^2 = 0.699 \quad \text{d.f.} = 9 \quad P = 0.025$$

No significant correlation ($r^2 < 0.3$, $P > 0.05$) was found for the rest of the year, nor was one found for any other size class of animals in the same season.

Lipids: Lipids showed a similar seasonal pattern in the

Table 2

Two-factor analysis of variance for gonad biochemical components of *Argopecten purpuratus*. Season and size are the main effects considered. ns, not significant; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

	d.f.	F
Proteins		
season	3	21.19***
size	2	14.34***
interaction	6	8.08***
residual	59	
Carbohydrates		
season	3	41.69***
size	2	15.07***
interaction	6	5.44***
residual	59	
Lipids		
season	3	20.47***
size	2	1.25 ns
interaction	6	1.15 ns
residual	53	

three size classes of scallops (Figure 3C, Table 2), although for the smallest individuals, one-way ANOVA showed no statistical difference between seasons. The winter lipid levels were always significantly lower (with the above-mentioned exception) than the other seasonal values.

Comparative analysis between female and male portions of ripe gonads: In summer, the gonads of 50- and 80-mm-length scallops appeared ripe, and female and male portions were analyzed separately for biochemical composition. For these two size classes of animals, female portions showed significantly higher protein and lipid levels than male portions (Table 3). There was no difference in carbohydrate levels between the two gonadal portions of the same size class of scallops. The carbohydrate content in the female gonadal portion of 80-mm-length specimens was higher than in the female portion of 50-mm-length specimens (one-way ANOVA, $F = 26.62$, $P < 0.001$).

Mantle Analyses

Protein: Protein was the main biochemical constituent of mantle tissue (Figure 4). Two-factor analysis of variance (Table 4) showed there was no overall seasonal variation but, rather, a clear size effect on protein content. In every season except summer, protein mantle content was always significantly lower ($P < 0.05$) in 80-mm-length individuals than in smaller ones (Appendix 3). One-way ANOVA for the smallest scallops showed significant seasonal differences ($F = 5.38$, $P < 0.05$) which a Tukey test showed to reside in lower summer than autumn and winter values.

Carbohydrates: Mantle carbohydrate content exhibited a clear seasonal pattern of changes (Figure 4B). Moreover,

Table 3

Protein, carbohydrate, and lipid levels of male and female portions of ripe gonads of two size classes of scallops. Values are means \pm SD ($n = 5$). ns, not significant; $*0.01 < P < 0.05$; $**0.001 < P < 0.01$; $***P < 0.001$.

	Male	Female	F
50-mm length			
proteins	452.73 \pm 13.58	567.69 \pm 45.59	5.84*
carbohydrates	5.03 \pm 0.63	4.78 \pm 0.57	0.08 ns
lipids	89.69 \pm 7.69	176.94 \pm 27.64	9.24*
80-mm length			
proteins	394.94 \pm 25.98	612.98 \pm 39.22	21.49**
carbohydrates	6.86 \pm 1.28	8.06 \pm 0.26	0.81 ns
lipids	87.37 \pm 5.79	245.90 \pm 22.45	46.75***

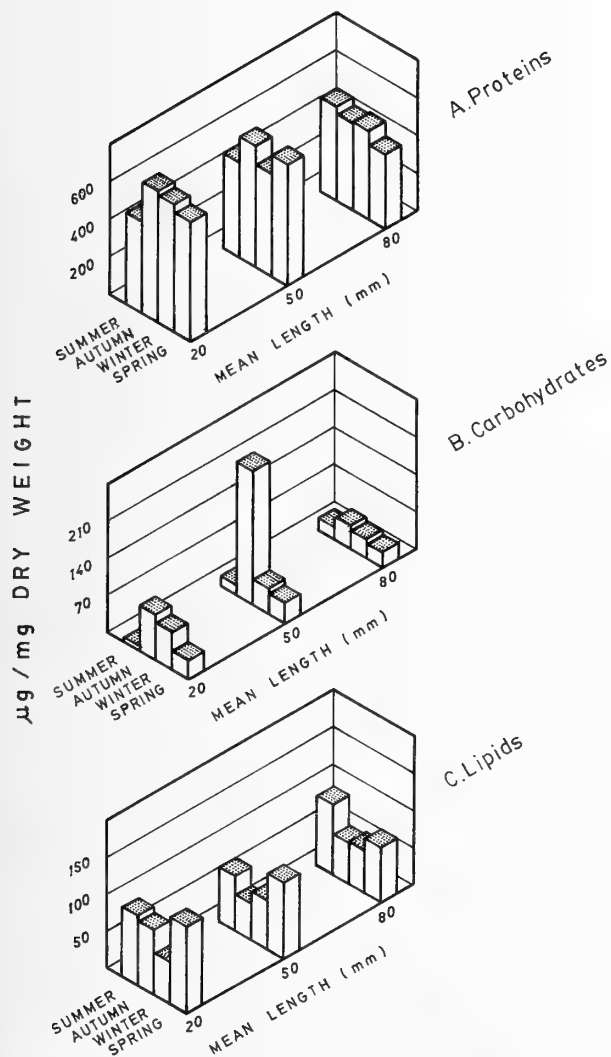


Figure 4

Seasonal changes in protein (A), carbohydrate (B) and lipid (C) contents of mantle tissue of three size classes of *Argopecten purpuratus*.

carbohydrate level not only changed with respect to season, but also with individual size (Table 4). In 50-mm animals, a very high value ($248.67 \pm 62.50 \mu\text{g}/\text{mg}$ dry wt.) occurred in autumn, contrasting with a very low summer level in the smallest scallops amounting to only $5.98 \pm 1.23 \mu\text{g}/\text{mg}$ dry wt.

In general, each size class of individuals showed the maximum carbohydrate level during autumn and the minimum in summer. In spite of a significant difference between summer and autumn ($P < 0.05$), the largest specimens showed smaller seasonal variations in this organic constituent than did the other two size classes of scallops.

Lipids: Mantle lipid content followed a clear seasonal pattern (Figure 4C) which was independent of the size class of the animals (Table 3). After summer, values decreased during the autumn and winter and increased in

Table 4

Two-factor analysis of variance for mantle biochemical components of *Argopecten purpuratus*. Season and size are the main effects considered. ns, not significant; $*0.01 < P < 0.05$; $**0.001 < P < 0.01$; $***P < 0.001$.

	d.f.	F
Proteins		
season	3	1.28 ns
size	2	19.87***
interaction	6	3.00*
residual	60	
Carbohydrates		
season	3	46.12***
size	2	28.43***
interaction	6	25.75***
residual	60	
Lipids		
season	3	9.14***
size	2	2.53 ns
interaction	6	1.99 ns
residual	55	

the spring. This increase was significant only in 20- and 50-mm-length individuals ($P < 0.05$).

DISCUSSION

Argopecten purpuratus is reproductive all year, with spawning peaks occurring in late summer and autumn (BROWN & GUERRA, 1982; DISALVO *et al.*, 1984; WOLFF, 1988). This pattern coincides with the gonad indices of adult scallops presented here, which showed maximal mean values in summer decreasing towards autumn, although not attaining indices as low as in winter. Nevertheless, in mid-length specimens a peak occurred only during summer, although this mean gonad index was well below the mean value shown by the largest scallops. According to the growth curve of *A. purpuratus* (DISALVO *et al.*, 1984), 45- to 55-mm-length individuals are still in a rapid phase of growth, so we may consider this size class to be experiencing both somatic and germinal growth.

In contrast to the observations by DISALVO *et al.* (1984) of gonadal material in specimens as small as 13 mm in length and the induction of spawning in individuals ranging in length from 21 to 27 mm, we did not find mature scallops under 25 mm in length. Moreover, our gonad indices showed very low values throughout the year, such that, in this context, we may consider animals of these size classes to be in a nonreproductive stage of their life cycles. Individuals 75 to 85 mm in length, which are in a slow-growing phase (DISALVO *et al.*, 1984), besides representing the major population mode in the natural banks (SERPLAC, unpublished data), are considered adult (reproductive) individuals.

The biochemical composition of adult *Argopecten purpuratus* showed a seasonal course whose most relevant feature was a decrease of carbohydrate content in the body components examined, associated with an increase of gonadal indices and high gonadal lipid and protein levels. This seasonal course is similar to that followed by other marine bivalves. It comprises a storing of energy substrates during a reproductively quiescent period and their subsequent utilization to support gametogenesis (GABBOTT, 1976, 1983; GIESE, 1966, 1969; SASTRY, 1979; BARBER & BLAKE, 1981, 1985).

In the adductor muscle of adult scallops, protein content rose in spring after remaining fairly constant the rest of the year. A similar rise in this constituent level of phasic adductor muscle at the time of gonad restoration has been reported for *Pecten maximus* by FAVERIS (1987). Studies on *Chlamys septemradiata* by ANSELL (1974), *Chlamys opercularis* by TAYLOR & VENN (1979), *Argopecten irradians concentricus* by BARBER & BLAKE (1981), and *Argopecten irradians irradians* by EPP *et al.* (1988), among others, have shown that these pectinids store protein and carbohydrate in their adductor muscle as an energy reserve for gametogenesis.

The spring rise in adductor muscle protein found in adult *Argopecten purpuratus* does not necessarily mean that

this biochemical component is the energetic substrate for gametogenesis, because 20- and 50-mm-length individuals also showed high values in the spring. Moreover, the smallest specimens had already attained this level during winter, and mid-sized animals increased their muscle protein content in autumn coincident with a fall of the gonad index, which remained low the rest of the year.

The largest variations in *Argopecten purpuratus* muscles were found in the carbohydrate content, with low levels in summer and winter and higher levels in autumn and spring. This pattern was similar for gonads and for the three size classes of individuals examined. Spring increases in the three biochemical constituents analyzed might be explained by an increase of phytoplankton abundance during this season (URIBE, 1989). The higher level of carbohydrate could represent the storage of reserves that the largest scallops would utilize for gametogenesis, the smallest for somatic growth, and the mid-sized individuals for both processes. DISALVO *et al.* (1984) showed that rapid growth of *A. purpuratus* occurs during the spring.

In relation to the utilization of carbohydrates for gametogenesis, BARBER & BLAKE (1985) have stated that during the initial stages of this process, the bay scallop *Argopecten irradians concentricus* catabolizes primarily carbohydrates and, as gametes mature and spawning begins, metabolism shifts to protein as the primary substrate. Sexual maturation in *Pecten maximus* occurs to the detriment of the phasic adductor muscle, which suffers a depletion of glycogen content (FAVERIS, 1987). Similar data have been reported for other pectinid bivalves such as *Chlamys septemradiata* by ANSELL (1974), *Chlamys opercularis* by TAYLOR & VENN (1979), and *Placopecten magellanicus* by ROBINSON *et al.* (1981). In *A. purpuratus* I have found very low carbohydrate levels during the summer when the gonad is ripe and the individual is ready to spawn. The inverse correlation between gonad index and carbohydrate content in reproductively mature individuals indicates that, in *A. purpuratus* as in other scallop species, carbohydrates are important for the maturation of gametes.

Lipids represent less than 10% of the dry weight in the muscle and mantle of adult *Argopecten purpuratus* and remain fairly constant throughout the year. They are always more abundant in the gonad, however, and experience great seasonal variations in this tissue related to oocyte development. Although these changes are not statistically significant in nonreproductive individuals, the lowest values are found in winter and the highest in summer coincident with the maximal gonad index. Similar results were obtained for *Chlamys opercularis* where muscle lipid content showed no clear seasonal change but increased greatly in the gonad during maturation (TAYLOR & VENN, 1979). High lipid levels were found in the ovary of *Placopecten magellanicus* from April until November, and then dropped as a result of spawning (ROBINSON *et al.*, 1981). *Chlamys tehuelcha* showed an increase in lipid content of the gonad in November–December and again in February–March coincident with a semiannual spawning cycle (POLLERO *et*

al., 1979). BESNARD (1987, 1988) stated that total lipid and triglyceride contents in the gonad of *Pecten maximus* faithfully reflect the course of sexual maturation, with highest levels being found during the period when oocytes are ready to be fertilized, thus assuring larval development. A high lipid content has also been reported in several bivalve larvae and its importance as an energy reserve has been established by HOLLAND & SPENCER (1973), MANN & GALLAGER (1985), and WHYTE *et al.* (1987).

The importance of lipid as an energy source in the planktonic eggs and larvae of marine bivalves is clearly demonstrated in the different biochemical compositions of ripe female and male gonad portions of *Argopecten purpuratus*. This pectinid showed a lipid content at least twice as large in the female portion as in the male portion. These results are comparable with those obtained for *Chlamys septemradiata* by ANSELL (1974) and for *Placopecten magellanicus* by THOMPSON (1977) and ROBINSON *et al.* (1981); in both species the ripe female gonad showed approximately twice as much lipid as the male. Nevertheless, in these pectinids, protein content in female gonads was less than in male gonads. In *A. purpuratus*, the protein level was higher in the female portion of the gonad than in the male. This difference might be related to the different reproductive characteristics of these pectinids: *A. purpuratus* is a functionally hermaphroditic bivalve, whereas *P. magellanicus* and *C. septemradiata* are dioecious. In *A. irradians concentricus*, another functionally hermaphroditic pectinid, the study of seasonal biochemical composition did not examine male and female gonad portions separately (BARBER & BLAKE, 1981; EPP *et al.*, 1988).

Analyses of the mantle tissue showed some surprising results, with clear differences occurring among the three size classes of *Argopecten purpuratus*. Nonreproductive specimens had high carbohydrate and protein levels during the autumn and winter. A second bloom of phytoplankton during autumn has been detected in Herradura Bay (URIBE, 1989), and these results might indicate that these smaller scallops store nutrients in the mantle.

The present study suggests that biochemical components of adult *Argopecten purpuratus* follow a seasonal cycle related to reproductive activities. Carbohydrate represents the major storage substrate utilized for gametogenesis and varies inversely with gonadal maturity. Lipids are accumulated in the ripe gonad to supply the metabolic needs of future larvae. The seasonal pattern differs between scallops in nonreproductive and reproductive stages and between reproductive and growing stages of the life cycle, reflecting complex interactions among age, food supply, temperature, growth, and gametogenesis.

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APPENDIX 1

Seasonal values for protein, carbohydrate, and lipid levels ($\mu\text{g}/\text{mg}$ dry wt.) of adductor muscle of three size classes of *Argopecten purpuratus*. Values are means \pm SD.

Size	20 mm	50 mm	80 mm
Protein			
summer	496.7 \pm 50.9	514.6 \pm 89.9	487.6 \pm 61.6
autumn	458.2 \pm 68.9	604.2 \pm 88.7	459.4 \pm 58.3
winter	590.6 \pm 29.1	428.7 \pm 54.4	480.9 \pm 29.4
spring	605.7 \pm 31.8	583.9 \pm 67.0	570.1 \pm 83.8
Carbohydrate			
summer	31.8 \pm 11.9	51.5 \pm 12.5	64.4 \pm 56.1
autumn	87.7 \pm 31.7	131.9 \pm 58.5	86.8 \pm 23.5
winter	86.5 \pm 38.8	33.0 \pm 25.8	40.7 \pm 26.0
spring	141.9 \pm 53.4	115.3 \pm 88.7	188.7 \pm 39.2
Lipid			
summer	67.4 \pm 4.5	62.9 \pm 12.2	55.1 \pm 10.0
autumn	62.9 \pm 18.2	45.2 \pm 15.6	64.0 \pm 30.5
winter	59.8 \pm 18.3	44.1 \pm 9.4	41.5 \pm 14.9
spring	72.1 \pm 20.8	72.0 \pm 13.1	59.7 \pm 10.7

APPENDIX 2

Seasonal values for protein, carbohydrate, and lipid levels ($\mu\text{g}/\text{mg}$ dry wt.) of gonad tissue of three size classes of *Argopecten purpuratus*. Values are means \pm SD.

Size	20 mm	50 mm	80 mm
Protein			
summer	444.2 \pm 68.1	419.7 \pm 64.1	531.7 \pm 67.8
autumn	611.1 \pm 55.7	609.2 \pm 46.8	462.9 \pm 62.6
winter	661.1 \pm 98.7	398.5 \pm 68.4	324.8 \pm 95.9
spring	753.6 \pm 99.4	610.4 \pm 93.2	599.9 \pm 98.1
Carbohydrate			
summer	53.6 \pm 10.8	46.9 \pm 11.6	26.2 \pm 21.1
autumn	119.3 \pm 48.8	159.4 \pm 26.4	72.6 \pm 14.5
winter	53.9 \pm 24.6	37.6 \pm 17.1	31.9 \pm 14.7
spring	71.4 \pm 27.8	55.1 \pm 18.4	56.6 \pm 16.9
Lipid			
summer	130.9 \pm 35.3	135.0 \pm 40.9	170.6 \pm 25.4
autumn	118.5 \pm 46.9	127.1 \pm 25.8	164.9 \pm 33.0
winter	85.7 \pm 43.2	82.0 \pm 22.9	78.3 \pm 31.5
spring	172.3 \pm 53.1	173.7 \pm 43.8	183.2 \pm 57.9

APPENDIX 3

Seasonal values for protein, carbohydrate, and lipid levels ($\mu\text{g}/\text{mg}$ dry wt.) of the mantle tissue of three size classes of *Argopecten purpuratus*. Values are means \pm SD.

Size	20 mm	50 mm	80 mm
Protein			
summer	511.6 \pm 92.2	515.3 \pm 59.9	490.4 \pm 61.3
autumn	710.6 \pm 82.5	647.6 \pm 50.3	448.4 \pm 61.3
winter	702.8 \pm 78.3	553.1 \pm 99.2	476.9 \pm 98.1
spring	643.9 \pm 62.5	636.2 \pm 73.9	391.6 \pm 38.6
Carbohydrate			
summer	5.9 \pm 1.2	15.7 \pm 4.1	14.5 \pm 14.2
autumn	89.0 \pm 46.3	248.7 \pm 62.5	36.2 \pm 13.3
winter	76.9 \pm 68.5	47.2 \pm 33.1	33.8 \pm 19.7
spring	39.9 \pm 15.6	39.9 \pm 19.4	26.6 \pm 7.5
Lipid			
summer	95.7 \pm 26.5	77.4 \pm 18.8	90.2 \pm 26.4
autumn	86.5 \pm 31.5	56.3 \pm 18.6	59.0 \pm 26.5
winter	58.8 \pm 23.1	70.9 \pm 22.2	61.1 \pm 16.4
spring	117.2 \pm 33.5	119.0 \pm 30.4	75.0 \pm 11.3

The Family Galeommatidae (Bivalvia: Leptonacea) in the Eastern Atlantic

by

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Abstract. Two new species of the Galeommatidae are described from West Africa: *Galeomma coalita*, unusual for the genus in having valves that may close almost completely, and *Ephippodonta gregaria*, the first known representative of its genus in the Atlantic. *Galeomma coalita* and the European species *Galeomma turtoni* (probably also the South African species *Coleoconcha opalina*) have parasitic dwarf males attached to the mantle, whereas *E. gregaria* is hermaphroditic. The range of *Galeomma turtoni* also includes West Africa.

INTRODUCTION

The Galeommatidae are a family of small marine bivalves that have attracted the attention of malacologists for their unusual characters: a trend towards expansion of the mantle over the shell and the ability to crawl about on their foot. They are represented in the Indo-Pacific by many genera and species. Only two Atlantic species resemble the European *Galeomma turtoni* Sowerby, 1825, with a large ventral gape on the shell: the American *Aclistothyra atlantica* McGinty, 1955, and the South African *Coleoconcha opalina* Barnard, 1963. More species of Galeommatidae have now been described from Florida by MIKKELSEN & BIELER (1989) who provided detailed anatomical and biological data. Other genera and species from the eastern Atlantic have been assigned to the family, but without data on the living animals and, thus, with great uncertainty.

Collecting in West Africa has yielded new localities extending the known range of *Galeomma turtoni*, and material for two new species that are described herein. Field notes were taken on these and on European specimens of *Galeomma turtoni* collected alive.

Museum abbreviations used in this paper are: ANSP, Academy of Natural Sciences, Philadelphia; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Muséum National d'Histoire Naturelle, Paris; SAM, South African Museum, Cape Town; USNM, National Museum of Natural History, Washington.

TAXONOMY

Family GALEOMMATIDAE Gray, 1840

Galeommatidae (corrected name, herein, for Galeomatidae Nordsieck, 1969, incorrect original spelling) is a junior

homonym and synonym. Ephippodontidae (corrected name, herein, for Ephippiodontidae Scarlato & Starobogatov, 1979), type genus *Ephippodonta* Tate, 1889, is considered a synonym.

Genus *Galeomma* Turton, 1825

Original reference: TURTON, 1825:361, pl. 13, fig. 1.

Type species: *Galeomma turtoni* Sowerby in TURTON, 1825, by monotypy (see ICZN, Art. 69a, vii).

Synonym: *Parthenope* Scacchi, 1833 (type species: *P. formosa* Scacchi, 1833, by monotypy).

Galeomma turtoni Sowerby in Turton, 1825

Original reference: TURTON, 1825:361, pl. 13, fig. 1.

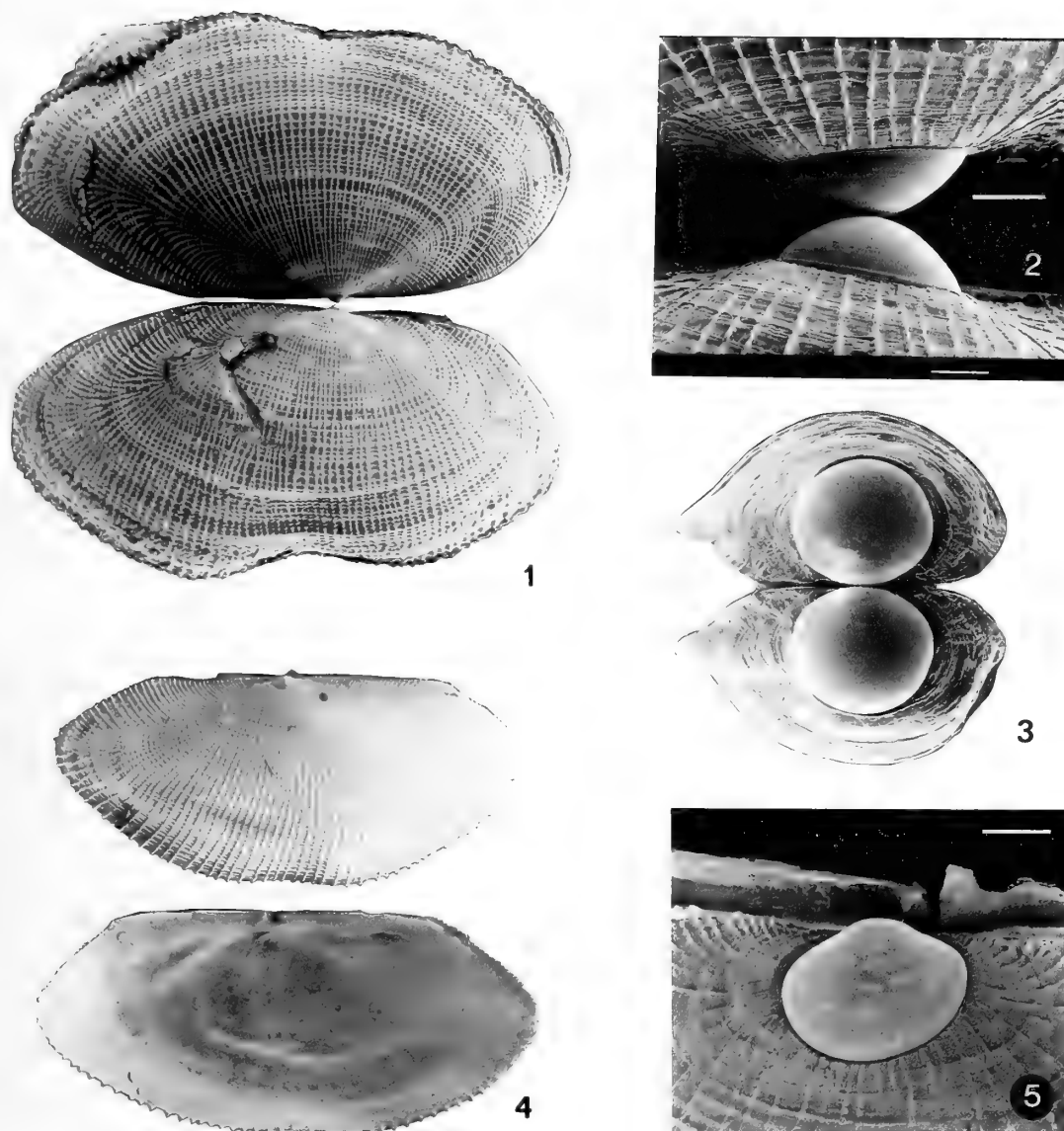
Type material: Holotype USNM 199412 (WARÉN, 1983:pl. 9, figs. 5–8).

Synonyms: “*Hiatella* de Poli” Costa, 1828 (vernacular); *Hiatella Poli* Costa in Scacchi, 1836, *Hiatella poliana* Costa in Philippi, 1844 (both first published as a synonym and not available).

Parthenope formosa SCACCHI, 1833:8–10, 19.

Galeomma pileum BRUSINA, 1866:42–43.

Material examined: European Atlantic and Mediterranean—Herm, Channel Islands, 4 shells (Staad collection, MNHN); Roscoff, Brittany, 2 shells (*leg.* Gofas 1976, MNHN); Guethary, Basque coast, Bay of Biscay, 3 specimens (*leg.* Gofas September 1988, MNHN); Sagres, Algarve, southern Portugal, 4 specimens (Mission Algarve, May 1988, MNHN); Cabo de Gata, Spain, 1 specimen (*leg.* Hergueta March 1986, MNCN); Marseille, 5 specimens (old collection MNHN); Marseille, 3 specimens (Jousseume collection, MNHN); Toulon, 4 specimens (Petit collection, MNHN); Giottani near Cap Corse, Corsica, 2 specimens (MNHN). New occurrences—Ouaran,



Explanation of Figures 1 to 5

Figures 1–5: *Galeomma turtoni* Sowerby in Turton.

Figure 1. Exterior of shell of adult female from Guethary, Bay of Biscay (actual length 8.6 mm).

Figure 2. Protoconch and initial part of teleoconch of the same specimen as in Figure 1 (scale bar is 100 μ m).

Figure 3. Shell of dwarf male attached to the same specimen as in Figure 1 (actual length 770 μ m).

Figure 4. Exterior of left valve and interior of right valve of a specimen from Cabo Ledo, Angola (actual length 5.4 mm).

Figure 5. Protoconch of specimen in Figure 4 (scale bar is 100 μ m).

near Dakar, Senegal, among rocks (*leg.* Bouchet August 1973, MNHN); Cabo Ledo, Angola, under stones taken in fishing nets 10–40 m, 2 specimens (*leg.* Gofas, MNHN).

Habitat: Inside large crevices in rocks or other hard substrata, from just below low tide level to ca. 20 m, crawling

free or byssally attached, generally isolated or in small numbers.

Selected measurements (in millimeters, length \times maximum height from umbo to margin):

Guethary	8.6 × 4.0	Marseille	13.4 × 6.3
	7.3 × 3.5		9.2 × 4.9
Algarve			9.2 × 4.3
	9.6 × 4.4		8.2 × 4.0
	8.8 × 4.3		8.1 × 4.3
	7.8 × 3.8		8.0 × 3.8
	6.3 × 2.9		
Herm		Corsica	6.7 × 3.3
	12.4 × 5.3		5.5 × 2.8
	10.8 × 5.2		
	10.6 × 5.1	Almeria	6.7 × 3.4
	10.3 × 5.1		

Remarks: The morphology and anatomy of this species have been described in detail by several authors, among them MITTRE (1847), PELSENEER (1911:44–45, pl. 16), and POPHAM (1940). BRUSINA (1866) distinguished *Galeomma pileum* as being shorter, more oval, and more markedly depressed laterally. This description is here considered to fall within the variability of *G. turtoni*.

Two specimens from Guethary, Bay of Biscay, have each been observed to host a dwarf individual attached to the ventral part of the mantle, near the edge of the valve. One of these has been sectioned (personal communication, G. Rodriguez, University of Oviedo). The large individual was a female. The small specimen has only a reduced foot and mantle, and a male gonad occupying its entire internal volume.

The shells of the other pair were photographed under SEM (Figures 1–3). The large shell is 9 mm long and has a smooth protoconch consisting of hemispherical valves 310 μ m in diameter. These are separated from the teleoconch by a sharp boundary, and the radial ribs of the teleoconch start exactly from that boundary. The smaller attached shell is 740 μ m long, with a protoconch similar in size and shape to that of the larger shell. Its teleoconch is very small, with sculpture consisting only of irregular, coarse growth lines, and no radial ribs.

A brooding specimen from Sagres, southern Portugal, was seen releasing spawn, eggs or small larvae less than 100 μ m in size, in May 1988. The morphology of the larval shell, with recognizable protoconch-1 and protoconch-2, and the abrupt protoconch-teleoconch boundary suggest that there is planktotrophic larval development.

Specimens collected in Angola (Figures 4, 5) are separated from the nearest northward locality (Ouaran, Senegal) by a large gap. The distribution of the species may be disjunct, like that of many West African bivalves (R. von Cosel, personal communication).

Galeomma coalita Gofas, sp. nov.

(Figures 6–8)

Type material: Holotype (MNHN), live-taken specimen and attached allotype: Caotinha, under stone at low tide mark, *leg.* Gofas, December 1985.

Paratypes (all *leg.* Gofas, 1983–1986, MNHN): An-

gola—Bango, 10 km S Ambrizete, province of Zaire, 1 valve (Figure 6); Praia São Tiago, province of Bengo, 1 valve; Barra do Dande, province of Bengo, 1 juvenile valve; São Nicolau, province of Namibe, 1 live-taken specimen (left valve crushed), under stone at low tide mark.

Type locality: Caotinha (12°36'S, 13°15'E), Benguela Province, Angola.

Other material examined: Senegal—Baie de Gorée, south of Tacoma, 25 m, 1 valve (*leg.* Marche-Marchad, MNHN); SE of Gorée, in fine muddy sand, 17 m, 1 valve (*leg.* von Cosel 24 March 1988, MNHN).

Habitat: The living specimens were found under stones, byssally attached to the rock surface.

Description: Shell 8–11 mm long, thin and fragile, equi-valve, slightly inequilateral with beaks anterior to the vertical midline. Outline oval-elongate with dorsal margin straight along ca. $\frac{7}{10}$ of the total length, anterior and posterior margins well rounded, and ventral margin nearly straight beneath the umbos. Protoconch with hemispherical valves, 300 μ m in diameter, smooth, demarcated from the teleoconch by a distinct line. Teleoconch with a reticulate external sculpture of radial riblets and concentric threads; the interspaces 2–3 times as broad as the riblets. Radial ribs divergent along the anterior and posterior slopes of the shell. Additional riblets added in the interspaces, and a few riblets terminating without reaching the margin of the shell. Shape laterally compressed, with valves almost closing ventrally.

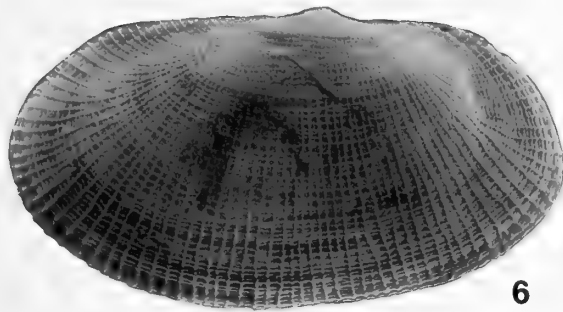
Hinge line smooth, interrupted under the umbo by a small resilifer, of different shape on the two valves. Left valve with a small vertical notch just beneath umbo and an oblique toothlike structure next to it posteriorly; right valve with a very oblique notch opposite to the toothlike structure of left valve, and hinge line abutting anteriorly to it with a small knob. Internal ligament short, in resilifer; external ligament thin, extending along hinge line.

Inside of valves with a broad, irregular, entire pallial line merging into the muscle scars. Scar of anterior adductor larger and closer to dorsal line than that of posterior adductor. Scar of posterior pedal retractor large, above the posterior adductor. Inner area beneath the umbo slightly granulated.

Mantle (Figure 8) thin and translucent, covering outer two-thirds of shell with tiny (ca. 200 μ m) papillae scattered over surface. One short tentacle attached at each end of hinge line.

Dwarf individual found attached by its foot to mantle of holotype, close to middle part of ventral margin: protoconch as above, teleoconch with leaf-shaped valves, gaping ventrally, pointed anteriorly and posteriorly, and with sculpture of coarse concentric growth lines only.

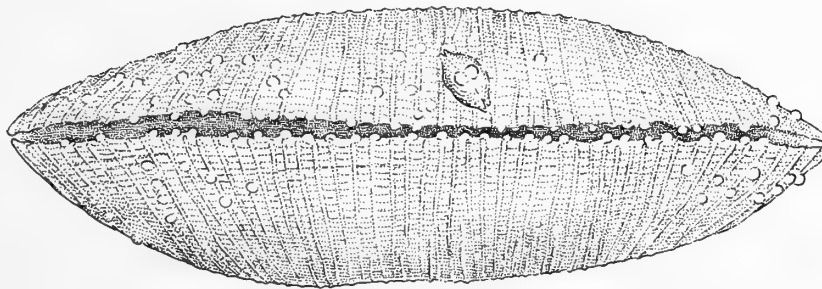
Selected measurements (in millimeters, length × maximum height from umbo to margin):



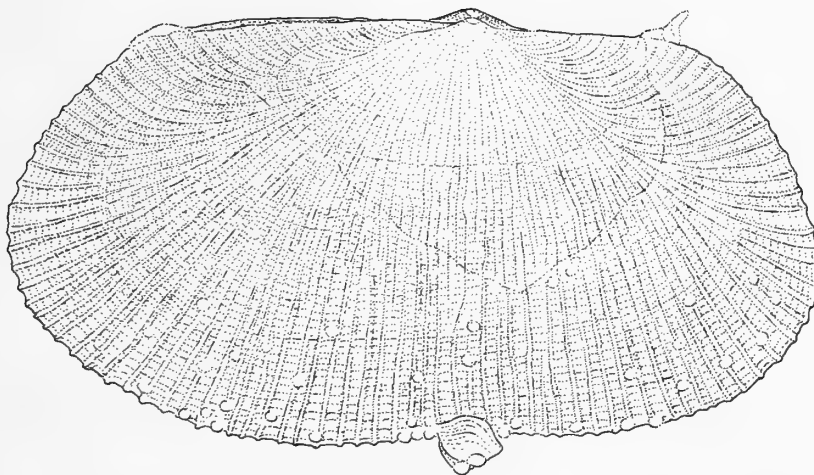
6



7



8



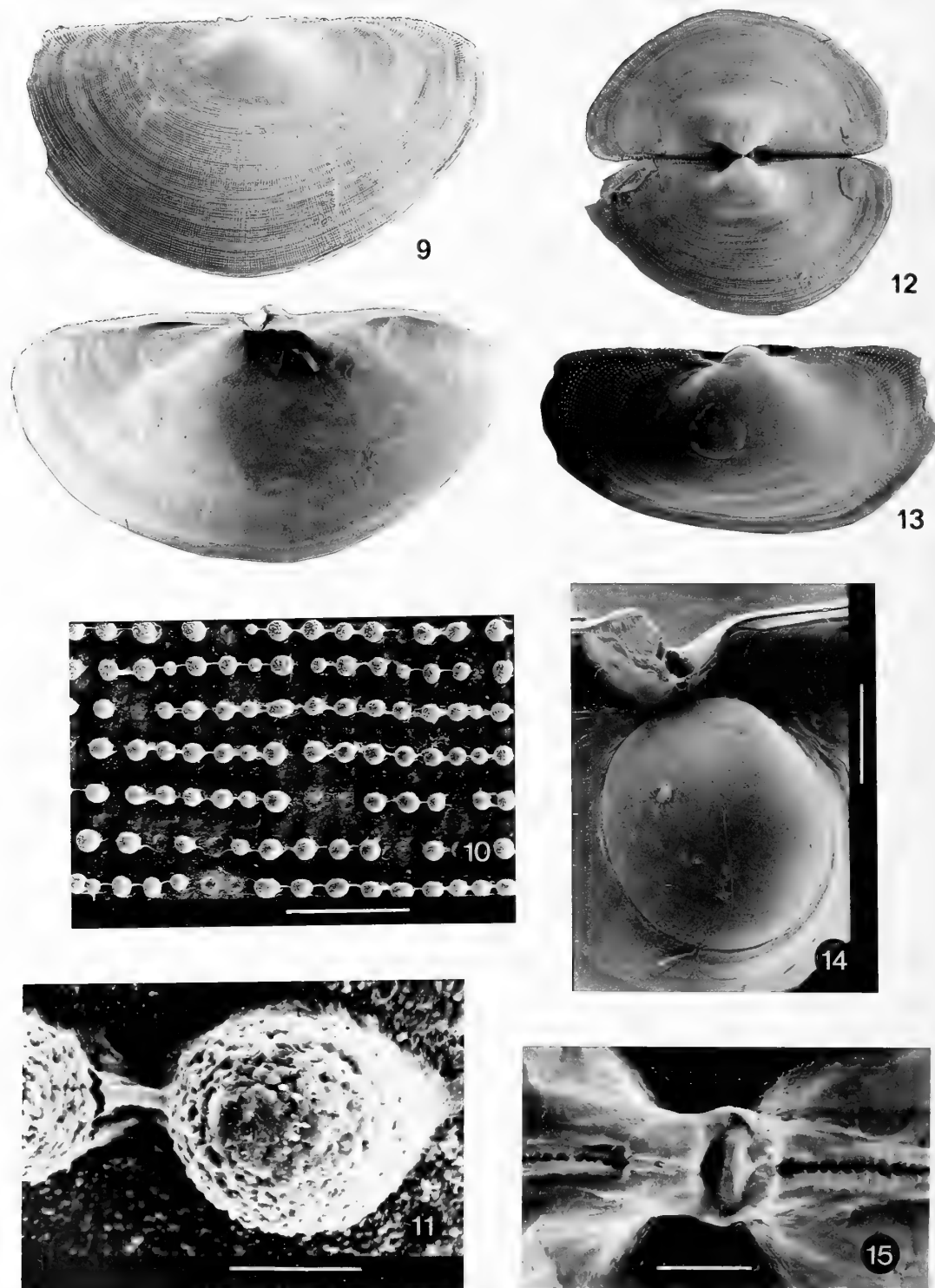
Explanation of Figures 6 to 8

Figures 6–8: *Galeomma coalita* Gofas, sp. nov.

Figure 6. Exterior of a paratype (right valve) from Bango, near Ambrizete, Angola (actual length 7.3 mm).

Figure 7. Detail of hinge and protoconch of a specimen from Bay of Gorée, Senegal (scale bar is 100 μ m).

Figure 8. Ventral view and lateral view of right side of the holotype from Caotinha, Angola (actual length 10.6 mm). Note attached dwarf male and membranous mantle covering the outer two-thirds of the shell.



Explanation of Figures 9 to 15

Figures 9–15: *Ehippodonta gregaria* Gofas, sp. nov.

Figure 9. Exterior of right valve and interior of left valve of the holotype from Cape Palmeirinhas, Angola (actual length 6.9 mm).

Figure 10. Detail of ornamentation of the holotype (scale bar is 100 μ m).

Caotinha (holotype)	10.6 × 5.5 and attached allotype 0.9
São Nicolau	10.0 × 5.0
Baie de Gorée	9.2 × 4.5
Bango	7.3 × 3.6 (Figure 6)
Praia São Tiago	7.8 × 4.0
SE of Gorée	6.9 × 3.6
Barra do Dande	4.0 × 1.9

Remarks: This species differs from *Galeomma turtoni* by being more compressed laterally, by its non-gaping valves, and by the much smaller size of the mantle papillae. The dwarf specimen is presumed to be a parasitic male as in *G. turtoni*. In *G. coalita*, it is attached to the outside, not beneath the valve edge as in *G. turtoni*. The hinge line is different in *G. turtoni*, where the small oblique resilifer is symmetrical. Details of ornamentation and sexual dimorphism are very similar to those in *G. turtoni*, and I consider that the species are congeneric.

Galeomma japonica Adams, 1862, type species of the genus *Pseudogaleomma* Habe, 1964, has a closing shell like *G. coalita*. It is otherwise reported to have a "granulated" sculpture, and nothing is known about its reproduction. More has to be known about *G. japonica* to decide if *Pseudogaleomma* may be synonymized with *Galeomma*.

Genus *Ehippodonta* Tate, 1889

Original reference: TATE, 1889:63–64.

Type species: *Scintilla(?) lunata* Tate, 1887, subsequent designation by MITCHELL, 1890:32.

Ehippodonta gregaria Gofas, sp. nov.

(Figures 9–18)

Type material: Holotype and 20 paratypes, all from the type locality (*leg.* Gofas and Fernandes, February 1987, MNHN); 5 paratypes, same locality (*leg.* Rolán, MNCN).

Type locality: North of Buraco inlet (09°05'S, 12°58'E), near Cape Palmeirinhas, Luanda Province, Angola.

Other material examined: Caotinha, province of Benguela, 1 juvenile specimen (*leg.* Gofas, MNHN).

Habitat: In crevices between rocks and the bases of large oysters *Striostrea denticulata* (Born, 1778), in 1–2 m depth below low tide. Specimens were found to line the cavity between the cemented oyster valves and the substratum,

aggregating in large numbers. No particular association was noted, but the cavities also hosted sponges and crustaceans.

Description: Shell 6–8 mm long, thin and fragile, equi-valve, almost equilateral. Outline oval-elongate with dorsal margin straight along ca. 1/10 of the total length, anterior and posterior margins well rounded, and ventral margin broadly rounded. Protoconch with hemispherical valves, with protoconch-1 hardly distinct, smooth, ca. 100 µm in diameter, and protoconch-2 ca. 270 µm in diameter, smooth, separated from the teleoconch by a distinct line. Teleoconch with a strongly inflated, smooth umbonal area, then rather flattened with external sculpture of tiny (20 µm) granules arranged regularly along concentric and radial lines. Granules connected along concentric lines by a fine thread; the interspaces slightly larger than the granules between concentric rows, smaller between radial lines. Radial rows of granules divergent along the anterior and posterior slopes of the shell, with additional radial lines of granules added there in the interspaces. Transverse profile with valves normally opened at ca. 180° when alive, unable to close completely because of hinge and ligament structure.

Center of hinge line with two strong toothlike thickenings symmetrically developed on each valve and abutting against each other but not interlocking; the anterior one larger, the posterior one small and mucronate. Resilium strong, permanently bent to maintain the valves open, wedged in between the toothlike thickenings. Remainder of hinge with minute crenulations, irregularly spaced and not clearly alternating nor facing each other.

Inside of valves (Figure 17) with a broad, irregular, entire pallial line merging into the muscle scars. Scar of anterior adductor slightly closer to dorsal line than that of the posterior adductor. Scar of posterior pedal retractor large, above the posterior adductor.

Mantle (Figure 16) covering entire shell, equipped with large (200–500 µm) pedunculate papillae scattered over dorsal surface, and fingerlike tentacles of comparable size forming fringe along edge of valves. One tentacle at each end of hinge line, small at rest but projecting to several times its original size when animal is immersed in formalin. Two pallial openings next to these tentacles, the posterior one smaller and closed, the anterior one connected ventrally with a large pedal gape. Ventral part of mantle smooth, with a definite groove parallel to the edge of the valves and its central part swollen. Foot elongated, capable of crawling, with a ventral longitudinal groove.

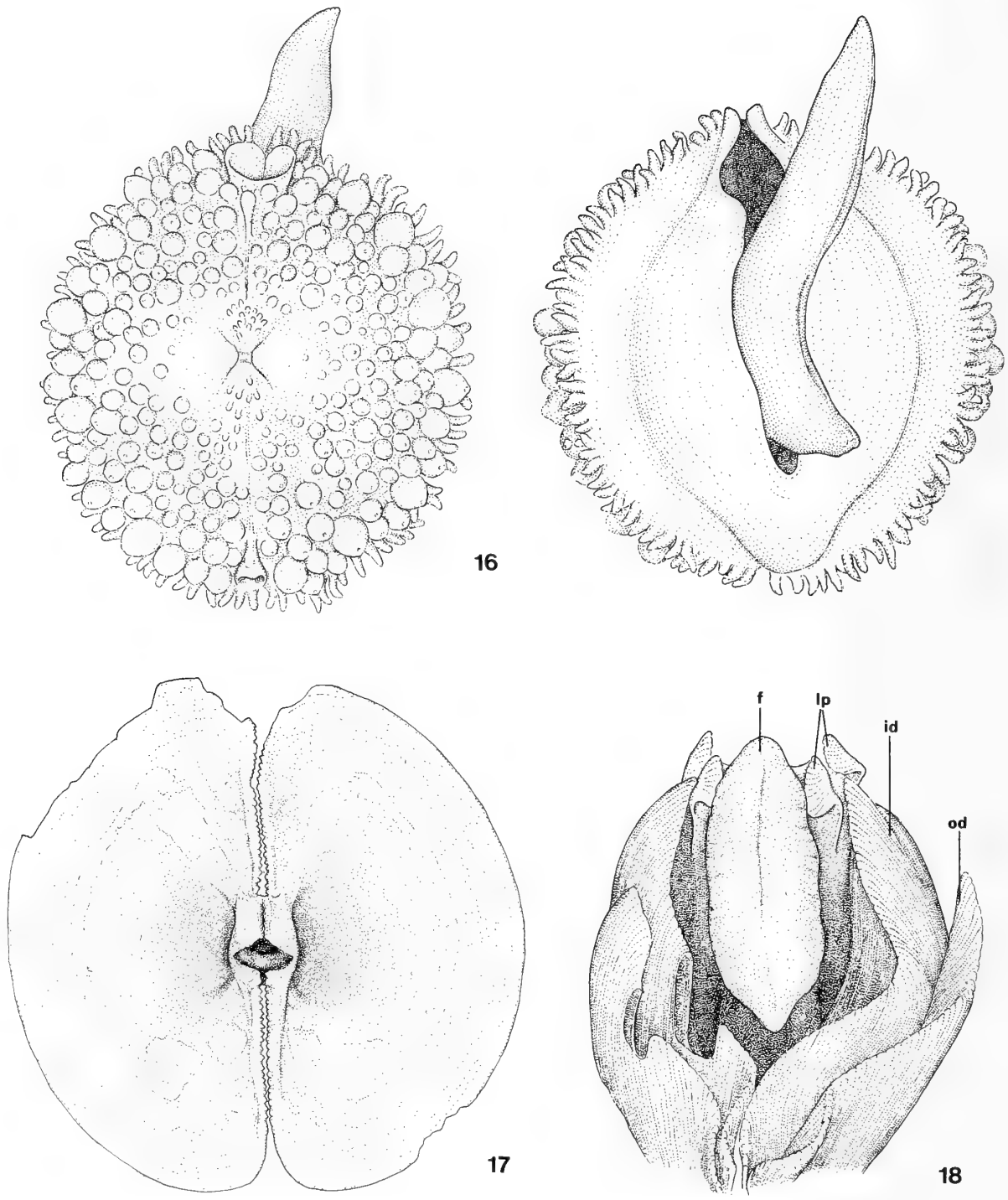
Figure 11. One of the granules, magnified (scale bar is 10 µm).

Figure 12. Exterior of the shell of a paratype (actual length 5.0 mm).

Figure 13. Left valve of another paratype (young specimen) showing smooth umbonal area (actual length 2.5 mm).

Figure 14. Protoconch of another paratype (arrow indicates protoconch-1/protoconch-2 boundary; scale bar is 100 µm).

Figure 15. Detail of hinge of another paratype (scale bar is 500 µm).



Explanation of Figures 16 to 18

Figures 16–18: *Ehippodonta gregaria* Gofas, sp. nov.

Figure 16. Dorsal and ventral view of a living specimen from Cape Palmeirinhas, Angola (actual length, excluding foot, 7.0 mm; anterior end up).

Figure 17. Internal view of the shell of a paratype (same specimen as fig. 12) showing pallial line and muscle scars (actual length 5.0 mm).

Figure 18. Detail of gills (od, outer demibranch; id, inner demibranch), labial palps (lp), and foot (f) of a preserved specimen, mantle removed (scale bar is 1 mm).

Selected measurements (in millimeters, length \times maximum height from umbo to margin):

Cape Pal-	7.2 \times 3.6	6.3 \times 3.2
meirinhas:	7.2 \times 3.4	6.1 \times 3.1
	7.1 \times 3.2	5.7 \times 2.8
	6.9 \times 3.9 (holotype)	4.5 \times 2.7 (figured
	6.8 \times 3.1	paratype)

Remarks: This species closely resembles the type species of the genus, *Ehippodonta lunata* (Tate, 1887), in the shape of the valves and the type of shell ornamentation with nodules arranged radially and concentrically. Also similar is the hinge line with strong thickenings abutting against each other and with no definite teeth. The Angolan species differs in having still smaller granules ornamenting the shell. A gregarious occurrence was also noted for *E. lunata* by MATTHEWS (1893): "One occasionally finds immense numbers of minute *Ehippodonta* lining the [shrimp] burrows."

Ehippodonta murakamii Kuroda, 1945, (type species of the subgenus *Ehippodontina* Kuroda, 1945, by original designation) differs in having weakly developed but distinct teeth on its hinge line. KURODA's (1945) illustrations show a finely reticulate ornamentation of concentric threads and radial riblets; these diverge along an anterior and a posterior radial line and sometimes bifurcate, in a pattern very similar to that of *Galeomma turtoni*. ARAKAWA (1960: 57) states about *E. murakamii* that "the shells are never wrapped with the expanded mantle."

Ehippodonta (Ehippodontina) oedipus Morton, 1976, differs in having much smaller, non-pedunculate papillae on the mantle and a more *Galeomma*-like reticulate ornamentation on the shell.

No dwarf males have been found on the mantle of examined specimens of *Ehippodonta gregaria* sp. nov. Eight specimens were sectioned; all contained spermatozoa, and five of them also contained ovules, which indicates that the species is hermaphroditic (personal communication, G. Rodriguez, Oviedo). Five of these eight specimens contained larvae, less than 100 μ m in length and oval-elongate in shape, brooded in the gills. The full grown protoconch seen on the adult shell is much larger than those brooded larvae. There is a clear boundary (Figure 14) separating protoconchs 1 and 2, indicating a planktotrophic larval development.

The ability to extrude the two tentacles anterior and posterior to the hinge line was also reported for *Galeomma polita* (Deshayes, 1856) by MORTON (1976), and was interpreted as a defensive behavior.

I have examined one paratype (one valve, ANSP catalogue no. 194067) of *Aclistothyra atlantica* McGinty, 1955 (type species of *Aclistothyra* McGinty, 1955, by original designation). It is superficially similar to *Ehippodonta gregaria*, but the hinge line is not crenulated, there are no cardinal-teeth nor thickenings, the resilifer is small, and the valves are more flattened, not swollen in the umbonal area. The external sculpture is not "granular" as

ambiguously suggested in the original description, but minutely pitted, and the pits are arranged in an alternating pattern and not radially. The pits are larger and more irregularly arranged close to the edge of the shell, becoming smaller and more regular towards the umbo. This microsculpture is coarser than the granules of the Angolan species. The protoconch in *A. atlantica* is smooth with hemispherical valves, ca. 380 μ m in diameter, and is separated from the teleoconch by a distinct line. This is very similar to the condition in *Galeomma*, *Ehippodonta*, and *Coleoconcha*, and also suggests a planktotrophic larval development.

Genus *Coleoconcha* Barnard, 1963

Original reference: BARNARD, 1963:33.

Type species: *C. opalina* Barnard, 1963, by monotypy.

***Coleoconcha opalina* Barnard, 1963**

Original reference: BARNARD, 1963:33–35.

Material examined: Syntype, 1 live-taken specimen preserved in alcohol, South African Museum, Cape Town, catalogue no. SAM 29642, exposed side of Schaapen Island, Langebaan (Saldanha Bay), leg. R. Dick, 24 April 1962.

Remarks: The two larger specimens mentioned by BARNARD (1963:34) are at this time missing from the South African Museum (J. Pether, in litt.). The collecting data and dimensions of the specimen illustrated here (Figure 19) fit the "smallest specimen" mentioned by Barnard and identify it as a syntype.

The shell is badly damaged by acidic alcohol. The protoconch is smooth, with hemispherical valves about 500 μ m in diameter, and an abrupt protoconch-teleoconch boundary. The teleoconch shows mostly growth lines, with several marked growth stages, and a minute crenulation of the posterior edge of the valves. Similar crenulations also appear anteriorly and are repeated along growth stages, according to BARNARD's (1963) description and illustration of the largest syntype.

Coleoconcha opalina has low, broadly spaced mantle tubercles, a straight hinge line devoid of teeth, and conspicuous labial palps. It resembles *Galeomma* most closely because of these characters.

The "juveniles (protoconchs) attached symmetrically on either side of the mantle," 0.75 mm long, observed by BARNARD (1963) on the largest specimen are presumably dwarf parasitic males as in *Galeomma*.

LARVAL DEVELOPMENT AND SEXUAL STRATEGIES

The larval shell of bivalves reflects patterns of larval development in the same way as that of gastropods. That is, a visible boundary between a small protoconch-1 and a protoconch-2 is evidence for a pelagic, planktotrophic development. In accordance with this similarity, I have called

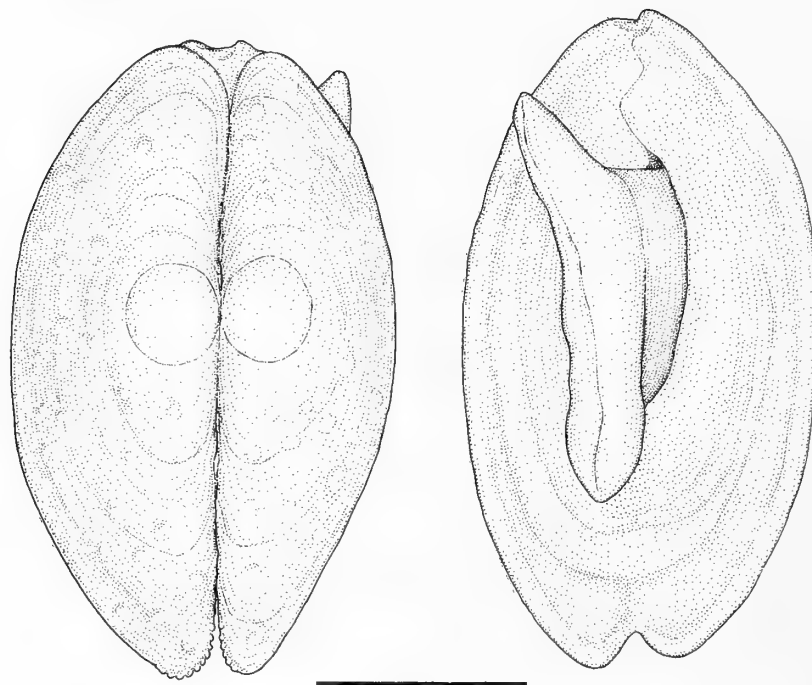


Figure 19

Coleoconcha opalina Barnard, 1963. Ventral and dorsal view of syntype (SAM 29642, actual length 3.0 mm, anterior end up).

the larval shell a "protoconch," notwithstanding the widespread use of the term "prodissoconch" in the literature on bivalves.

A sequence of brooding of larvae in the pallial cavity in an early stage and then pelagic development is inferred for *Galeomma turtoni* and *Ephippodonta gregaria*, on the grounds that larvae less than 100 μm in diameter were seen brooded or just released, whereas the protoconch on the adult shell is nearly 300 μm in diameter with a recognizable boundary between protoconch-1 and protoconch-2 (Figures 3, 5, 14). The release of "shell-less larvae" was also observed for *Galeomma turtoni* by POPHAM (1940).

Brooding followed by pelagic larval development is most common among the Leptonacea (LEBOUR, 1938; CHANLEY & CHANLEY, 1970; O'FOIGHIL, 1988; MIKKELSEN & BIELER, 1989; and references therein). A few species brood their larvae until they are released with so-called "direct" benthic development (e.g., DEROUX, 1960; OLDFIELD, 1964).

Dwarf males, attached to the outside of adult females, were seen in both Atlantic species of *Galeomma* and inferred to exist in *Coleoconcha*. The occurrence of parasitic dwarf males has been documented many times in the Leptonacea. Shelled dwarf males such as in *Galeomma* have been reported for *Ephippodonta oedipus* by MORTON (1976).

In *Montacuta phascolionis* Dautzenberg, 1925 (Leptonacea: Montacutidae), accessory dwarf males are brooded in

the pallial cavity with the larvae and maintain many larval features; the larger host individuals, however, also develop spermatozoa (DEROUX, 1960). Dwarf males have been reported associated with larger females in "*Pseudopythina*" *subsinuata* (Lischke, 1871) (MORTON, 1972), and brooded in the pallial cavity of "*Pseudopythina*" *rugifera* (Carpenter, 1864) (O'FOIGHIL, 1985). Both species are interpreted as protandric hermaphrodites, with further development of the male outside the female shell, and sex reversal. Extreme reduction of the males is seen in *Montacuta percompressa* (Dall, 1899), where they are reduced to shell-less masses of gonad, 500 μm in diameter, parasitic on the females (JENNER & MCCRARY, 1968).

In the case of *Galeomma* (Figures 2, 3), the initial part of the teleoconch differs between the "normal" shells of females and the shells of dwarf attached males. This means that sex is already determined at the time of settling and the dwarf males will not eventually grow into larger females. A likely scheme would be that sex determination is induced by the presence or absence of a female at the time of settling.

The taxonomic significance of the reproductive features is yet to be evaluated. Morphological similarity in the larval shells of planktotrophic *Galeomma*, *Aclistothyra*, *Ephippodonta*, and *Coleoconcha* are a clue to close a relationship. The family may also include, however, non-planktotrophic species and, in this case, protoconch morphology may be different. The occurrence of dwarf males

is not definitive at the family level; it has been documented in other, not closely related, small leptonacean bivalves (e.g., *Montacuta*). Conversely, all other characters suggest that the hermaphroditic *Ehippodonta gregaria* and the sexually dimorphic *Galeomma* should be placed in the same family. If one assumes that *Ehippodonta oedipus* is a true *Ehippodonta* and not a *Galeomma*, the occurrence of dwarf males is not even definitive within one genus.

A comparable array of sexual strategies is documented for the Eulimidae, a family of small gastropods parasitic on echinoderms (WARÉN, 1984). The possible advantages of sexual dimorphism for a parasite stated by WARÉN (1984:24) do not obviously apply to the case of Galeommatidae where dwarf males were seen on free-living *Galeomma*. The association of a dwarf male may well be advantageous for any species (parasite or not) where planktotrophic development ensures easy dispersal of larvae and, as with *Galeomma*, the adults are scattered, isolated individuals.

ACKNOWLEDGMENTS

Material for this study was collected with Francisco Fernandes, of Luanda, Angola, during field work carried out in common from 1981 to 1987, and with Philippe Bouchet during the *Algarve* excursion of MNHN in 1988. Gonzalo Rodriguez (University of Oviedo, Spain) prepared histological sections of *Galeomma* and *Ehippodonta* and commented on them. John Pether (South African Museum) searched for the original material of BARNARD (1963) and sent it to me on loan. Gregorio Martín Caballero and Juan José Canca Cuenca (University of Malaga, Spain) assisted me with operating the SEM. Philippe Bouchet (MNHN), Rudo von Cosel (MNHN), Winston Ponder (Australian Museum), Anders Warén (Swedish Museum of Natural History), Rüdiger Bieler (Field Museum, Chicago), and an anonymous referee are thanked for critically reading the manuscript.

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A New Middle Eocene Potamidid Gastropod from Brackish-Marine Deposits, Southern California

by

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Abstract. The potamidid gastropod *Potamides (Potamidopsis) californica* sp. nov. is described from brackish-marine deposits in the middle Eocene Matilija Sandstone north of Reyes Peak and at Matilija Hot Springs, Ventura County, southern California. This is the first record of the subgenus *Potamidopsis* in North America. Previously, it was known from uppermost Paleocene and middle Eocene deposits of France.

INTRODUCTION

The potamidid gastropod *Potamides (Potamidopsis)* previously has been known only from uppermost Paleocene and middle Eocene deposits in France (GLIBERT, 1962: 161-162). This brackish-marine gastropod has now been found in two areas within the middle Eocene Matilija Sandstone in Ventura County, southern California, and is here described as *Potamides (Potamidopsis) californica* sp. nov. The early through middle Eocene was a time of influx of many Old World mollusks and other invertebrates into the Pacific coast region of North America by way of Central America (SQUIRES, 1984, 1987), and *Potamidopsis* can now be added to this growing list of taxa.

Abbreviations used for catalog and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology Section; SDSNH, San Diego Society of Natural History; UCLA, University of California, Los Angeles (collections now housed at the LACMIP).

MATERIALS AND METHODS

The type locality of the new species is locality LACMIP 7226 in the Beartrap Creek area, Ventura County, southern California (Figure 1). Approximately 25 specimens were collected from this locality in the 1930s by paleontologists associated with the California Institute of Technology. These specimens, which are now housed at the LACMIP, are the best preserved material of the new species, and the primary type material used in this report was selected from them. Most of the specimens of the new species from the type locality are poorly preserved.

Approximately 60 specimens of the new species were collected also from the Beartrap Creek locality by JESTES (1963), who referred to the locality as UCLA 4254. These specimens are now stored at the LACMIP. I visited the locality in late 1990 and found a few specimens of the new species in float. The source bed of the float, however, could not be found because recent landslides had covered the outcrops.

This new species is also found near Matilija Hot Springs (Figure 1). Most specimens were collected from nearly vertical exposures along a roadcut. JESTES (1963) did some collecting from two localities (LACMIP 24258 and 24259) in these deposits and the specimens are now housed at the LACMIP. I have been recollecting from JESTES' two localities since 1980 and have recently found an additional locality (CSUN 1444) in the same area and another locality (CSUN 1450) along strike of the same beds a short distance to the north (Figure 1). No other outcrops of the beds were found. Abundant specimens of *Potamides (Potamidopsis) californica* were found at localities CSUN 1444, CSUN 1450, and LACMIP 24258, but only a few specimens were found at locality LACMIP 24259. All of the specimens of the new species at the Matilija Hot Springs area are obscured due to coating by well indurated siltstone.

STRATIGRAPHIC OCCURRENCES AND DEPOSITIONAL ENVIRONMENTS

In the vicinity of the Beartrap Creek locality is a section of several hundred meters of fine- to coarse-grained micaceous sandstone with local conglomerate (JESTES, 1963) that was mapped as part of the Matilija Sandstone by

VEDDER *et al.* (1973) and GIVENS (1974). On the basis of mollusks, GIVENS (1974) correlated the Matilija Sandstone in this area to the "Tejon Stage." SAUL (1983) and SQUIRES (1988) regarded the "Tejon Stage" as mostly middle Eocene in age with a small part assigned to the late Eocene.

At the Beartrap Creek locality, JESTES (1963) reported that the fossils were in a 60-cm-thick bed of coarse-grained calcareous sandstone. In addition to scattered pebbles, he found mudrock chips and some wood fragments. Some shell fragments are present, and some of the gastropod shells showed preferred orientation. Float from the now-covered outcrops reveals that the bed also contains very poorly sorted conglomeratic sandstone with single valves of bivalves and large fragments of oysters up to 10 cm in length. Fossils show evidence of transport, but the distance of transport was not great because indications of significant abrasion are absent.

JESTES (1963) interpreted the environment of deposition at the Beartrap Creek locality to be a mixture of brackish and nearshore marine on the basis of the types of mollusks. In addition to a few specimens of the freshwater bivalve *Unio*(?) *torreyensis* (Hanna, 1927), he found many specimens of the three brackish-marine mollusks: the bivalve *Cuneocorbula torreyensis* Hanna, 1927, and gastropods *Loxotrema turritum* Gabb, 1868, and *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869. All of these mollusks have been found in middle Eocene brackish-marine deposits elsewhere on the Pacific coast of North America (VOKES, 1939; GIVENS, 1974; GIVENS & KENNEDY, 1976; SQUIRES, 1987). JESTES (1963) also reported the presence of *Potamides* sp., herein assigned to *Potamides* (*Potamidopsis*) *californica*. Modern potamidid gastropods are confined to brackish-marine estuaries (KEEN, 1971).

The other mollusks found at the Beartrap Creek locality by JESTES (1963) are nearshore-marine mollusks. Examples include the bivalves *Acutostrea* cf. *A. idriaensis* Gabb, 1869, *Lucina* sp., *Crassatella* sp., and *Tivela* sp., and the gastropods *Turritella uvasana* Conrad, 1855, and *T. merriami*? Dickerson, 1913. All of these mollusks have been found in Eocene nearshore-marine or shelfal deposits elsewhere on the Pacific coast of North America (VOKES, 1939; GIVENS, 1974; SQUIRES, 1987, 1989).

The mixed assemblage at the Beartrap Creek locality must have been the result of storms that admixed brackish-marine and nearshore-marine species.

At the Matilija Hot Springs area, where the type section of the Matilija Sandstone is located, there is a 40-m-thick section of evaporites, red beds, limestone, lignite?, mudcracks, and interbedded shell accumulations (LINK, 1975; LINK & WELTON, 1982). These workers, as well as DIBBLEE (1987), mapped the section as the Matilija Sandstone. Based on the presence of planktonic foraminifers and coccoliths in the overlying Cozy Dell Formation, LINK & WELTON (1982) assigned the Matilija Sandstone to the middle Eocene P11 and P12 Zones.

The four localities from which specimens were collected in the Matilija Hot Springs area are similar in that each

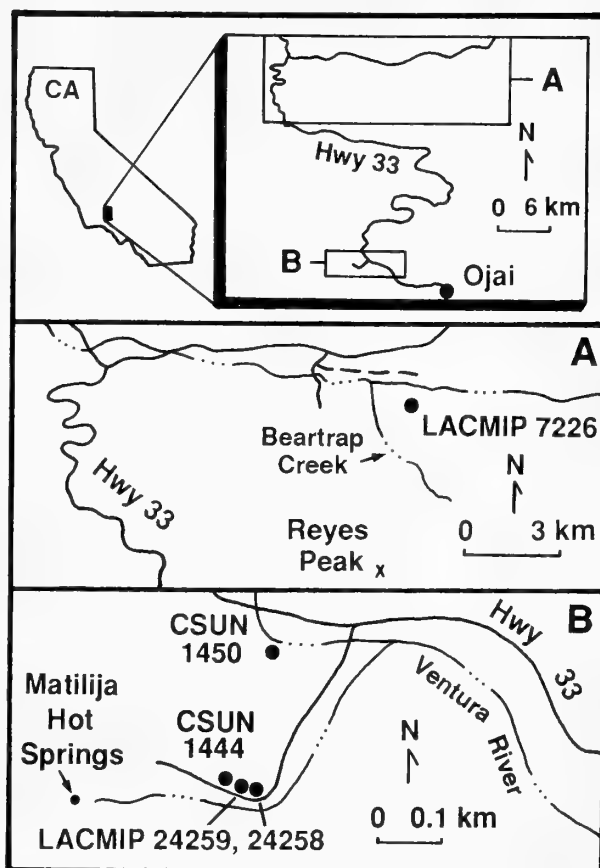


Figure 1

Geographic occurrences of *Potamides* (*Potamidopsis*) *californica* Squires, sp. nov., in southern California. A. Beartrap Creek area. B. Matilija Hot Springs area.

one is associated with 10-cm-thick siltstone or sandy siltstone beds surrounded by fine to very fine, well sorted and cross-bedded sandstone with scattered ostreid fragments. Specimens of all the mollusks at the four localities seem to be unabraded and show growth series. JESTES (1963) said the mollusks may be dwarfed, but normal-sized specimens of each taxon can be found. Many of the infaunal bivalves are articulated. The bivalve *Cuneocorbula torreyensis* forms coquinooids of unbroken single valves, as well as some articulated valves, at localities LACMIP 24258 and 24259. Some sort of concentration of the *Cuneocorbula torreyensis* shells must have taken place by means of waves or currents, but the distance of transport was short. At the other two localities, the distance of transport seems to be minimal.

JESTES (1963) interpreted the environment of deposition at the Matilija Hot Springs localities to be brackish marine on the basis of the types of mollusks. He found nearly all of the same brackish-marine species that he found at the Beartrap Creek locality. Jests' findings of the following brackish-marine taxa are corroborated in this present work: the bivalves *Cuneocorbula torreyensis* and *Corbicula* sp., and

the gastropod *Loxotrema turritum*. His *Ostrea* sp. is *Acuostrea idriaensis fettkei*? (Weaver, 1912). He also found an articulated specimen of a bivalve he identified as *Unio*?. Although it is an unionid and indicative of freshwater conditions, it is too poorly preserved to be assigned to any genus (C. Coney, personal communication). JESTES (1963) also reported the presence of *Potamides* aff. *P. tricarinata* (Lamarck, 1804), herein assigned to *Potamides* (*Potamidopsis*) ***californica***. The faunas at each of the four localities are generally similar, but the numbers of individuals of different species vary greatly. The only species that is present in the upper half but not in the lower half of the 35-m-thick section is *Cuneocorbula torreyensis*.

LINK (1975) and LINK & WELTON (1982) used the preliminary studies of JESTES (1963) as the basis for their faunal analysis at the Matilija Hot Springs area. On the basis of a sedimentological study, and supported by JESTES' (1963) findings of brackish-marine mollusks, LINK (1975) and LINK & WELTON (1982) determined that most of the Matilija Sandstone in the vicinity of Matilija Hot Springs is a deep-sea fan sequence but that the upper part is a shallow-marine sequence representing a coastal (paralic) environment. These paralic deposits are the ones that yield *Potamides* (*Potamidopsis*) ***californica***. LINK & WELTON (1982) interpreted the siltstone in these deposits as being associated with lagoons and the sandstones as being associated with beach-bar-channel complexes.

SYSTEMATIC PALEONTOLOGY

Family POTAMIDIDAE H. & A. Adams, 1854

Subfamily POTAMIDINAE H. & A. Adams, 1854

Genus *Potamides* Brongniart, 1810

Type species: By monotypy, *Potamides lamarchi* Brongniart, 1810.

Subgenus *Potamidopsis* Munier-Chalmas, 1900

Type species: By original designation?, *Cerithium tricarinatus* Lamarck, 1804.

Potamides (*Potamidopsis*) ***californica***

Squires, sp. nov.

(Figures 2–5)

Diagnosis: A *Potamidopsis* whose whorls have reticulate sculpture consisting of three equal-strength spiral ribs crossed by numerous axial ribs.

Description: Medium sized, turritelliform, with at least 10 concave-sided whorls, slightly coeloconoid. Protoconch unknown. Suture obscured by overhanging spiral sutural rib. Whorls strongly angulated near anterior suture by a carina, gently sloping above with three equal-spaced and approximately equal-strength spiral ribs. Interspaces with or without a single spiral thread. Whorls crossed by nu-

merous opisthocline axial ribs of nearly same strength as spiral ribs. Nodes at intersections of spiral and axial ribs produce a reticulate sculpture pattern. Posteriormost spiral rib nodes usually slightly stronger than on the other two spiral ribs. Sutural spiral rib immediately posterior to suture and with or without nodes. Carina with prominent nodes where axial ribs intersect. Area anterior to carina on body whorl with two sharp and unnoded spiral ribs, the posterior one strongest. Area anterior to these two spiral ribs (*i.e.*, base of body whorl) with four to five weaker and unnoded spiral ribs. Columella short. Aperture missing.

Holotype: LACMIP 11300.

Type locality: Locality LACMIP 7226, Beartrap Creek area, Ventura County, southern California, (119°16'30"W, 34°40'48"N).

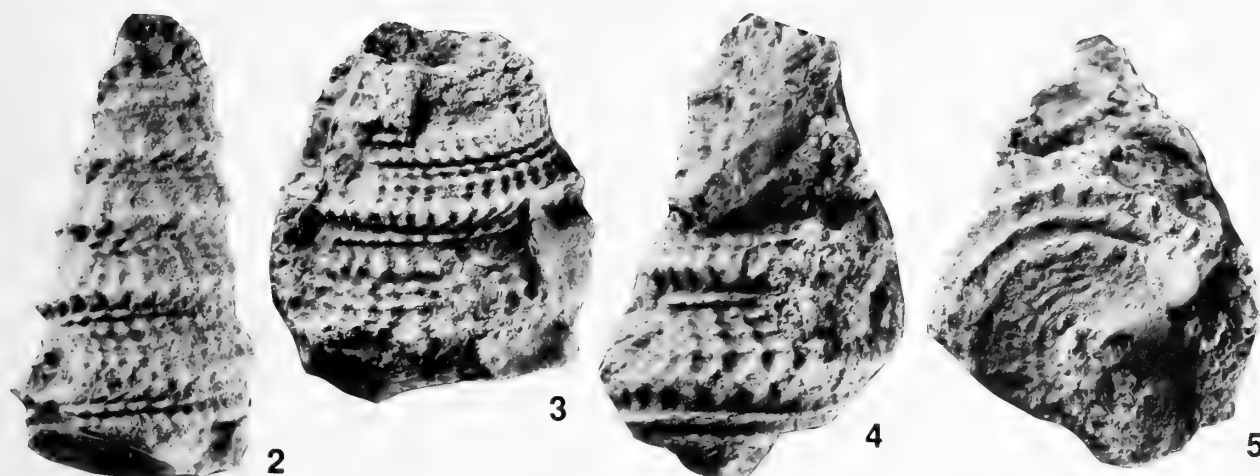
Paratypes: LACMIP 11301 and 11302.

Dimensions: Of holotype (incomplete), height 20 mm, width 11 mm; of paratype 11301 (incomplete), height 13.8 mm, width 10 mm; of paratype 11302 (incomplete), height 13 mm, width 8.5 mm.

Discussion: The new species was compared with all six previously known species of *Potamidopsis*. All are from France, with most occurrences in the Paris Basin. One is the rare *P. (P.) pourcyensis* COSSMANN (COSSMANN, 1913: pl. 2, fig. 151–36; COSSMANN & PISSARRO, 1910–1913: pl. 65, fig. 151–36) from uppermost Paleocene deposits, and the other five are from middle Eocene deposits (Lutetian and/or Bartonian Stages) (GLIBERT, 1962:161–162). They are *P. (P.) tricarinatus* (LAMARCK, 1804:272; DESHAYES, 1833:pl. 51, figs. 1–9), *P. (P.) mixtus* (DESHAYES, 1833:pl. 45, figs. 6–11; COSSMANN & PISSARRO, 1910–1913:pl. 28, figs. 151–12 and 151–12'), *P. (P.) depontaillieri* (COSSMANN, 1881:168, pl. 7, fig. 4; COSSMANN, 1889:69–70, pl. 2, figs. 11–12; COSSMANN & PISSARRO, 1910–1913: pl. 28, fig. 151–13), the rare *P. (P.) andrei* (VASSEUR, 1881: pl. 6, figs. 9, 15–16; COSSMANN, 1897:pl. 10, figs. 11, 17; 1898:9–10), and the rare *P. (P.) ripaudi* (VASSEUR, 1881: pl. 5, figs. 9–20; pl. 19, figs. 10–11; COSSMANN, 1898:10–11, pl. 2, figs. 2, 5).

The new species differs from all of these species of *Potamidopsis*, except *Potamides (P.) andrei* and *P. (P.) ripaudi*, by possessing reticulate sculpture. The new species most closely resembles *P. (P.) andrei*. On the basis of comparisons with two LACMIP specimens of *P. (P.) andrei* from Bois Gouet, France, the new species differs in having (1) a much larger shell that is heavier and thicker, (2) reticulate sculpture that is more strongly developed, (3) less numerous and less closely spaced axial ribs, (4) a sutural rib immediately posterior to the suture, and (5) a much more swollen anterior carina.

On the basis of comparisons with five LACMIP specimens of *Potamides (P.) ripaudi* from Bois Gouet, France,



Explanation of Figures 2 to 5

Figures 2–5. *Potamides (Potamidopsis) californica* Squires, sp. nov., locality LACMIP 7266. Figure 2: holotype, LACMIP 11300, lateral view, $\times 3.1$. Figure 3: paratype, LACMIP 11301, lateral view, $\times 3.6$. Figures 4 and 5: paratype, LACMIP 11302, $\times 4.8$. Figure 4: lateral view. Figure 5: oblique lateral view showing base of body whorl.

the new species differs in having (1) a larger shell that is heavier and thicker, (2) three rather than two spiral ribs, (3) a much more swollen anterior carina, (4) no tendency for the anterior carina to be absent on the upper spire, (5) weaker axial ribs, (6) axial ribs opisthocline, (7) and no very fine spiral riblets in interspaces.

The new species somewhat resembles *Potamides (P.) tricarinatus*. The new species was compared with 10 LACMIP specimens of *P. (P.) tricarinatus* from Fere-en-Tardenois, France. These specimens have the range in morphology shown in the illustrations (COSSMANN & PISSARRO, 1910–1913:pl. 28, figs. 151–11, 151–11', 151–11'', 151–11''', 151–11''') of the several varieties of this species. The new species differs from *P. (P.) tricarinatus* in the following features: (1) three rather than none to two spiral ribs, (2) equal-strength spiral ribs, (3) the presence of axial ribbing, (4) the presence of reticulate sculpture where the axial ribs intersect the spiral ribs, and (5) an anterior carina that is generally not as strong. One particular specimen of *P. (P.) tricarinatus* illustrated in COSSMANN & PISSARRO (1910–1913:pl. 28, fig. 151–11) approaches the reticulate sculpture of the new species, but the new species has three rather than two spiral ribs posterior to the carina and has stronger nodes on the carina.

Although four species of Eocene *Potamides* have been reported previously from the Pacific coast of North America, only one actually belongs to *Potamides*. It is *Potamides (Potamides?) carbonicola* Cooper (COOPER, 1894:44, pl. 1, figs. 14–29) known from lower Eocene to upper Eocene strata in California (VOKES, 1939; GIVENS, 1974; GIVENS & KENNEDY, 1976) and from middle Eocene strata in western Oregon and western Washington (TURNER, 1938; WEAVER, 1943). The new species was compared with the

descriptions and illustrations of *Potamides (Potamides?) carbonicola*. The illustrations and emended description in GIVENS & KENNEDY (1976:963–964, pl. 1, figs. 9–13) are particularly useful. The new species also was compared with many specimens of *P. (P.?) carbonicola* from three widely separated locations on the Pacific coast of North America. Some of these specimens are in collections of the LACMIP and SDSNH, and some are in my private collection. The locations are the Lookingglass Formation, Glide, southwestern Oregon; the Domengine Formation, Griswold Canyon, Vallecitos syncline area, central California; and the Del Mar Formation?, Vista, San Diego County, southern California.

The new species differs from *Potamides (P.?) carbonicola* in the following features: (1) the upper spire whorls concave rather than flat-sided, (2) reticulate sculpture persisting beyond only the uppermost spire whorls, (3) the anterior carina representing the strongest sculpture everywhere on teleoconch, (4) no tabulate carina in the posterior region of mature whorls, (5) no tendency for the posteriormost spiral rib to equal the carina in strength, (6) no varices on the upper spire, and (7) nodosity does not become obsolete.

The three other Eocene "*Potamides*" species from the Pacific coast of North America are all from the Cowlitz Formation of southwestern Washington, and they belong to genera other than *Potamides*. GIVENS & KENNEDY (1976) assigned *Potamides fettkei* Weaver, 1912, to *Melanoides* (family Thiaridae) and assigned *Potamides lewisiana* Weaver, 1912, to *Elimia* (Family Pleuroceridae). *Potamides packardi* (Dickerson, 1915) is very closely related to "*Potamides*" *lewisiana* and is herein regarded as also assignable to *Elimia*.

Occurrence: Middle Eocene Matilija Sandstone, Ventura County, southern California: at Beartrap Creek area (locality LACMIP 7226) and at Matilija Hot Springs area (localities CSUN 1444, CSUN 1450, LACMIP 24258, LACMIP 24259).

ACKNOWLEDGMENTS

George L. Kennedy (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) arranged for access to the LACMIP collection and loans of specimens. Thomas A. Deméré (Natural History Museum of San Diego County) arranged for access to the SDSNH collection. Clif Coney (Natural History Museum of Los Angeles County, Malacology Section) examined the unionid bivalve specimen.

LOCALITIES CITED

Unless otherwise specified, localities are in the NE¼ of the SE¼ of section 29, T5N, R23W, Matilija quadrangle (7.5 minute), 1952 (photorevised, 1967), in the vicinity of Matilija Hot Springs, Ventura County, southern California.

CSUN 1444. Roadcut on N side of a short, paved road that leads from Highway 33 to Matilija Hot Springs, about 35 m W of sharp bend in this road, near bottom of brackish-marine deposits, in a nonresistant interval.

CSUN 1450. About 120 m SW of junction of Highway 33 and short, paved road that leads to Matilija Hot Springs, on S bank of North Fork of Matilija Creek, near bottom of brackish-marine deposits, in a fairly nonresistant interval.

LACMIP 24258. Approximately at sharp bend in short, paved road that leads from Highway 33 to Matilija Hot Springs, near top of brackish-marine deposits, in a resistant interval 16 m stratigraphically above locality LACMIP 24259. Locality is the same as UCLA 4258 of JESTES (1963).

LACMIP 24259. About 16 m W of sharp bend in short, paved road that leads from Highway 33 to Matilija Hot Springs, near middle of brackish-marine deposits, in a resistant interval 19 m stratigraphically above locality CSUN 1444. Locality is the same as UCLA 4259 of JESTES (1963).

LACMIP 7226. Just E of hill 4560 along an unmaintained trail and downslope for about 15 m from trail, at section line between sections 24 and 25, T7N, R23W, Reyes Peak quadrangle (7.5 minute), 1943, in the vicinity of Beartrap Creek, about 5.6 km N5°E of Reyes Peak, Ventura County, southern California. Source beds not found but probably from near top of hill 4560. Locality is the same as UCLA 4254 of JESTES (1963).

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The Philadelphia Syntypes of *Ammonites hoffmanni* Gabb (Cretaceous) (Mollusca: Ammonoidea)

by

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Abstract. Two syntypes of *Ammonites hoffmanni* Gabb, 1864, at the Academy of Natural Sciences of Philadelphia were inadvertently overlooked when a lectotype was chosen by MURPHY & RODDA (1977). These two specimens, and at least two others as yet unidentified, formed the basis of Gabb's composite illustrations for this species. The two syntypes belong to two taxa: The smaller syntype (ANSP 4794a) is designated a paralectotype of *A. hoffmanni* [= *Puzosia hoffmanni* (Gabb)], and the larger syntype (ANSP 4794b) is assigned to *Mesopuzosia colusaense* (Anderson, 1902).

INTRODUCTION

In a previous paper (MURPHY & RODDA, 1977) we described the 10 syntypes of *Ammonites hoffmanni* Gabb, 1864, in the University of California, Museum of Paleontology, Berkeley (UCMP). We chose one of these (UCMP 12094) as the lectotype of *A. hoffmanni*; three other syntypes were designated paralectotypes (UCMP 14154, 14839, 14921). The other six syntypes were assigned to five different ammonite taxa: *Puzosia subquadrata* (Anderson, 1902), UCMP 14155; *Melchiorites indigenes* Anderson, 1938, UCMP 14156, 14157; *Melchiorites shastensis* Anderson, 1938, UCMP 14158; *Melchiorites* sp., UCMP 12091; and *Lytoceras argonautarum* Anderson, 1902, UCMP 14153. We inadvertently overlooked two

syntypes of *A. hoffmanni* at the Academy of Natural Sciences of Philadelphia (ANSP 4794) (RICHARDS, 1968: 212). The purpose of this paper is to describe, illustrate, and discuss these two additional syntypes. For comparisons we have used other specimens from the geology collections of the California Academy of Sciences (CASG). Measurements of all cited specimens are presented in Table 1.

HISTORY

From 1862 to 1868 W. M. Gabb was a paleontologist for the Geological Survey of California (Whitney Survey), and he described many fossil species collected from Cretaceous and Cenozoic rocks of California (GABB, 1864, 1869). When the California Legislature terminated the Whitney Survey

Explanation of Figures 1 to 6

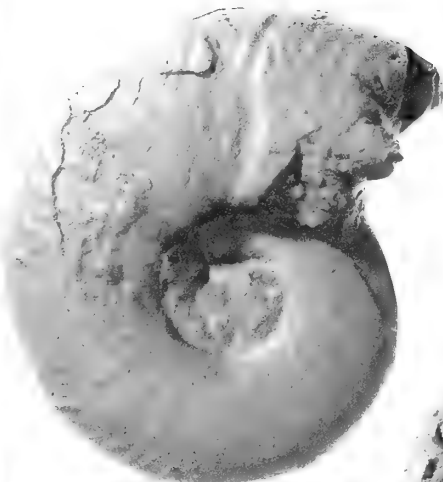
Figures 1, 2. *Ammonites hoffmanni* Gabb, 1864. Figure 1. Reproduction of GABB's figure (1864:pl. 11, fig. 13); original drawing 85 mm high. Figure 2. Reproduction of GABB's figure (1864:pl. 11, fig. 13a); original drawing 35 mm high.

Figures 3, 4. *Puzosia hoffmanni* (Gabb, 1864). Paralectotype, ANSP 4794a, maximum diameter 56 mm. Figure 3. Apertural view. Figure 4. Lateral view.

Figures 5, 6. *Mesopuzosia colusaense* (Anderson, 1902). Hypotype (*ex* syntype of *Ammonites hoffmanni* Gabb, 1864), ANSP 4794b, maximum diameter 127 mm. Figure 5. Lateral view. Figure 6. Apertural view.



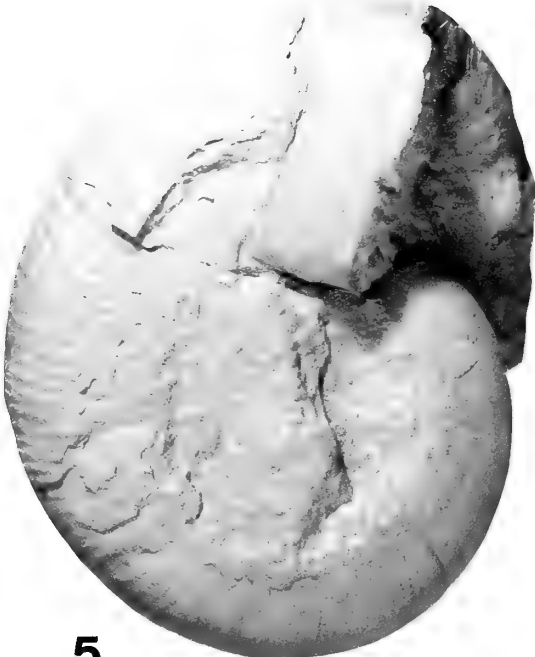
1



2



3



5



6

Table 1

Measurements of lectotype and paralectotypes of *Ammonites hoffmanni* Gabb, 1864 [= *Puzosia hoffmanni* (Gabb)], and of other cited specimens. Abbreviations are as follows: D, shell diameter; H, whorl height; W, whorl width; U, umbilical diameter. All measurements are in millimeters. Numbers in parentheses express measurements as percentages of shell diameter. Dashes indicate measurement could not be taken.

	D	H	W	U
<i>Puzosia hoffmanni</i> (Gabb, 1864)				
UCMP 12094 (lectotype)	110	42 (38)	45 (41)	39 (35)
ANSP 4794a (paralectotype)	56	23 (41)	19 (34)	16 (29)
UCMP 14154 (paralectotype)	57	22 (39)	22 (39)	20 (35)
UCMP 14839 (paralectotype)	43	18 (42)	16 (37)	12 (28)
UCMP 14921 (paralectotype)	43	18 (42)	17 (40)	14 (33)
<i>Mesopuzosia colusaense</i> (Anderson, 1902)				
CASG 4283 (holotype)	240	106 (44)	88 (37)	61 (25)
CASG 10798 (hypotype)	145	65 (45)	45 (31)	38 (26)
ANSP 4794b (hypotype)	127	56 (44)	41 (32)	— (—)

in 1868, Gabb deposited a large collection of California fossils at the Academy of Natural Sciences of Philadelphia; other survey fossils were deposited later at the University of California, Museum of Paleontology, and at Harvard University, Museum of Comparative Zoology (MERRIAM, 1895; STEWART, 1926). These collections include the type specimens of many California fossil species.

STEWART (1926, 1930) reviewed Gabb's species of gastropods and bivalves, and designated type specimens, but there is no such comprehensive treatment for Gabb's California fossil cephalopods. ANDERSON (1938) describes some of Gabb's California Cretaceous ammonites that were deposited at the Museum of Paleontology (UCMP) and at Philadelphia (ANSP). ANDERSON (1938) examined several of Gabb's specimens of *Ammonites hoffmanni* at the Museum of Paleontology, but he either overlooked the two syntypes at Philadelphia, or they were not available at that time. However, Anderson's designation of a lectotype for *A. hoffmanni* (ANDERSON, 1938:187, pl. 45, figs. 1, 2) is invalid because he did not choose a specimen from the existing syntypes (MURPHY & RODDA, 1977:78). Subsequently, we selected a valid lectotype from the 10 syntypes at the University of California, Museum of Paleontology, Berkeley (MURPHY & RODDA, 1977:79).

SYSTEMATIC DISCUSSION

The two ANSP syntypes are assigned to two species. The smaller syntype (ANSP 4794a) is conspecific with *Puzosia hoffmanni* (Gabb, 1864) as characterized by MURPHY &

RODDA (1977), and the larger syntype (ANSP 4794b) is identified as *Mesopuzosia colusaense* (Anderson, 1902).

MOLLUSCA

CEPHALOPODA

Family DESMOCERATIDAE Zittel, 1895

Subfamily PUZOSIINAE Spath, 1922

Genus *Puzosia* Bayle, 1878

Puzosia hoffmanni (Gabb, 1864)

(Figures 1–4)

Ammonites hoffmanni GABB, 1864:65, pl. 11, figs. 13, 13a, pl. 12, fig. 13b.

Desmoceras dilleri ANDERSON, 1902:97, pl. 4, figs. 116, 117, pl. 10, fig. 192.

Puzosia subquadrata (Anderson): ANDERSON, 1938:186 (in part), pl. 45, fig. 4.

Puzosia hoffmanni (Gabb): MURPHY & RODDA, 1977:79, figs. 1–5.

The small syntype (ANSP 4794a) has the whorl profile and cross-section, umbilical characteristics, ribbing, and constrictions of *Puzosia hoffmanni* (Gabb) (= *Ammonites hoffmanni* Gabb) as redefined by MURPHY & RODDA (1977). This syntype (ANSP 4794a) is here designated as a paralectotype of *A. hoffmanni*.

Genus *Mesopuzosia* Matsumoto, 1954

Mesopuzosia colusaense (Anderson, 1902)

(Figures 5–10)

Desmoceras colusaense ANDERSON, 1902:96, pl. 5, figs. 128, 129, pl. 10, fig. 200.

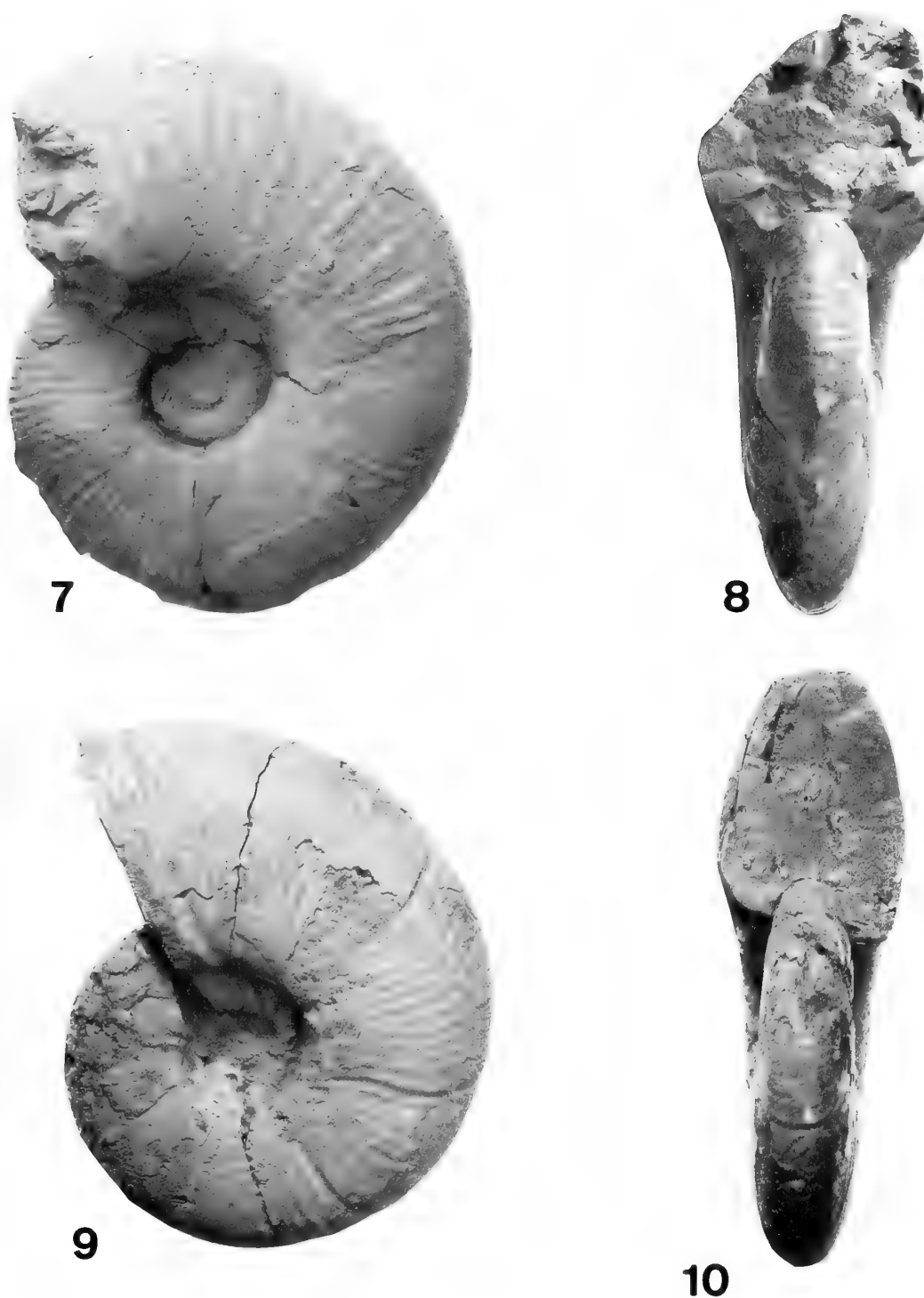
Puzosia (*Parapuzosia*) *colusaensis* (Anderson): ANDERSON, 1958:236, pl. 10, fig. 1.

Pachydesmoceras colusaense (Anderson): MATSUMOTO, 1959a:62; MATSUMOTO, 1959b:22.

Mesopuzosia colusaense (Anderson): MURPHY & RODDA, 1960:850, pl. 102, fig. 10.

The compressed whorl, narrow venter, and sigmoidal ribs of the larger syntype (ANSP 4794b) of *Ammonites hoffmanni* Gabb (Figures 5, 6) are similar to small specimens, or the internal whorls of larger specimens, of the puzosid ammonite *Mesopuzosia colusaense* (Anderson). The holotype of this species (CASG Type No. 4283; ANDERSON, 1902:pl. 5, figs. 128, 129) and Anderson's 1958 hypotype (CASG Type No. 10798; ANDERSON, 1958:pl. 10, fig. 1) are illustrated here for comparison (Figures 7–10). The holotype, a moderately large specimen (diameter 240 mm), is from the Petersen Ranch, near Sites, Colusa County, California. The hypotype was collected on the North Fork of Cottonwood Creek, Shasta County, California.

Remarks: Gabb's original description of *Ammonites hoffmanni* (GABB, 1864:65, pl. 11, figs. 13, 13a, pl. 12, fig. 13b) included three illustrations, a lateral view, a whorl



Explanation of Figures 7 to 10

Figures 7, 8. *Mesopuzosia colusaense* (Anderson, 1902). Holotype, CASG 4283, maximum diameter 240 mm. Figure 7. Lateral view. Figure 8. Apertural view.

Figures 9, 10. *Mesopuzosia colusaense* (Anderson, 1902). Hypotype, CASG 10798, maximum diameter 145 mm. Figure 9. Lateral view. Figure 10. Apertural view.

cross-section, and a suture line. The lateral view (pl. 11, fig. 13) is a lithograph of a finely ribbed ammonite about 130 mm in diameter, with numerous constrictions and a partly exposed umbilicus. The whorl cross-section (pl. 11, fig. 13a) is an outline drawing 35 mm high and 25 mm wide. Both of these illustrations are reproduced here (Figures 1, 2).

Figure 13 of GABB (1864:pl. 11) is a composite drawing based on at least three different specimens, the two syntypes at the ANSP (4794a, 4794b), and one or more as yet unknown specimens. The general outline of GABB's figure (1864:pl. 11, fig. 13) was taken from the larger syntype, ANSP 4794b. This specimen is about the same size as the illustration, has the same general outline, and has the same distinctive terminal fracture of the outer whorl (Figures 1, 5). However, unlike Gabb's original illustration, this specimen has a completely covered umbilicus. The partly exposed umbilicus of GABB's figure (1864:pl. 11, fig. 13) closely matches the umbilicus of the smaller syntype, ANSP 4794a (Figures 3, 4). The constrictions on GABB's figure (1864:pl. 11, fig. 13) do not exactly match those of either ANSP syntype, nor a combination of the two, in character or position. Gabb's illustration has 10 sigmoidal constrictions that are projected adapically on the ventrolateral area. The larger syntype (ANSP 4794b) has 10 constrictions projected *adorally* on the ventrolateral area; only the five inner constrictions agree in position with Gabb's illustration. The small syntype (ANSP 4794a) has eight constrictions, also projected adorally on the venter, that do not match the constrictions of GABB's figure (1864:pl. 11, fig. 13).

The small syntype (ANSP 4794a) has a whorl section similar to, but not identical with, that of GABB's figure (1864:pl. 11, fig. 13a); ANSP 4794a is smaller and slightly wider. The whorl section of the larger syntype (ANSP 4794b) has about the same proportion of height to width as the figured cross-section, but ANSP 4794b has a distinctly different cross-sectional shape with a narrower venter and a more trigonal outline (Figure 6). The suture line (GABB, 1864:pl. 12, fig. 13b) appears to have been taken from another, as yet undetermined specimen; no suture line is visible on either of the ANSP syntypes. In summary, Gabb used at least four different specimens to illustrate *Ammonites hoffmanni*, and one figure (GABB, 1864:pl. 11, fig. 13) is a composite drawing based partly on the two syntypes at the Academy of Natural Sciences of Philadelphia.

In choosing a lectotype, preference should be given to originally illustrated specimens if available (Recommendation 74B, International Code of Zoological Nomenclature). In the present case, when the lectotype of *Ammonites hoffmanni* Gabb was chosen (MURPHY & RODDA, 1977: 79), the existing, partly illustrated, Philadelphia syntypes were inadvertently overlooked. However, because of the composite nature of Gabb's illustrations, the interpretation of the ANSP syntypes described above is in taxonomic harmony with our previous designation of the lectotype,

and thus conforms, at least in spirit, to ICZN Recommendation 74B.

Distribution: On the old labels with the two syntypes at the ANSP, the collecting locality for both specimens is indicated as "Cottonwood Creek" (Shasta County, California). The only locality for *Ammonites hoffmanni* indicated in GABB (1864:65, 220) is "Horsetown," an old mining camp on Clear Creek, about 8 km northeast of the North Fork of Cottonwood Creek.

Fossils from the site of old Horsetown occur in dark gray sandstone within the *Breweriaceras hulenense* ammonite zone (MURPHY, 1956; MURPHY & RODDA, 1977). To our knowledge no specimens of *Puzosia hoffmanni* have been found at this locality or at this stratigraphic level. We have collected *Puzosia hoffmanni* from the North Fork of Cottonwood Creek and vicinity in fine-grained limy nodules scattered in mudstone and in the mudstone itself (Budden Canyon Formation of MURPHY *et al.*, 1969). The paralectotype (ANSP 4794a) has the fine-grained limy matrix typical of the North Fork occurrences.

Specimens of *Mesopuzosia colusaense* similar to the larger syntype (ANSP 4794b) of *Ammonites hoffmanni* have been collected from limy nodules in mudstone, and from sandstone and conglomeratic sandstone (Budden Canyon Formation), on Huling Creek and the North Fork of Cottonwood Creek, Shasta County, and on Dry Creek, Tehama County (MURPHY & RODDA, 1960; MURPHY *et al.*, 1969). The stratigraphic age of *M. colusaense* is significantly younger than any fossils known from the site of old Horsetown. The large syntype (ANSP 4794b) (= *M. colusaense*) has a matrix of yellow-brown, fine- to medium-grained sandstone that resembles the sandstones that crop out near the junction of the North Fork of Cottonwood Creek and Huling Creek.

In the Cottonwood Creek district, *Puzosia hoffmanni* and *Mesopuzosia colusaense* have different, non-overlapping stratigraphic ranges (MURPHY, 1956; MURPHY *et al.*, 1969; MURPHY & RODDA, 1977; RODDA & MURPHY, 1987). We have collected *Puzosia hoffmanni* from the *Gabbiceras win-tunius* zone through the *Leconteites lecontei* zone of early to middle Albian age (MURPHY, 1956; MURPHY *et al.*, 1969). *Mesopuzosia colusaense* is a suggested local guide fossil for rocks of latest Albian age (MURPHY *et al.*, 1969).

The two syntypes of *Ammonites hoffmanni* at the ANSP came from different stratigraphic levels, and both probably came from the North Fork of Cottonwood Creek or nearby. Neither specimen is likely to have been collected at old Horsetown.

In conclusion, 12 syntypes of *Ammonites hoffmanni* Gabb, 1864, representing seven different taxa, are at two depositories. The 10 specimens at the University of California, Museum of Paleontology are assigned to six different taxa, and UCMP 12094 was chosen as the lectotype (MURPHY & RODDA, 1977). The two specimens at the Academy of Natural Sciences of Philadelphia (ANSP 4794a, 4794b) belong to two taxa, and they demonstrate the composite

nature of Gabb's original illustrations. The smaller of these two syntypes (ANSP 4794a) is herein designated a paralectotype of *A. hoffmanni* Gabb, 1864 [= *Puzosia hoffmanni* (Gabb, 1864)]. The larger specimen (ANSP 4794b) is assigned to *Mesopuzosia colusaense* (Anderson, 1902).

ACKNOWLEDGMENTS

We are grateful to George Kennedy, Los Angeles County Museum of Natural History, for calling our attention to the ANSP specimens, and we thank George Davis, Academy of Natural Sciences of Philadelphia, for the loan of the two syntypes.

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NOTES, INFORMATION & NEWS

Corbula kelseyi Unmasked: A *Cumingia* (Bivalvia) by

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Corbula kelseyi has remained a puzzle since Dall described it in 1916 (DALL, 1916a:41, *nomen nudum*; 1916b:416). Indeed, the type specimen, a left valve measuring 16 mm in length from Catalina Island, California, has been illustrated only once (OLDROYD, 1925:204, pl. 3, fig. 9), with a marginally useful external view.

We have recently had an opportunity to examine the type specimen (USNM 120691), and it proves to be a worn valve of *Cumingia californica* Conrad, 1837. The sharp external sculpture and large pallial sinus suggested this assignment, and close comparison confirmed it. Other material assigned to *Corbula kelseyi* should undoubtedly be referred to other species of *Corbula*, most probably in the case of specimens from southern California, to *C. luteola* Carpenter, 1864.

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Pycnogonid Predation on Nudibranchs and Ceratal Autotomy

by
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Nudibranchs and other naked mollusks have long been known for their capacity promptly to autotomize pinched cerata (STASEK, 1967). This behavior is one of numerous defensive adaptations that perhaps make up for their in-

creased vulnerability due to the absence of a protective shell (EDMUNDS, 1966).

Naked opisthobranchs are also known to defend themselves by secreting toxins and noxious chemicals. Some nudibranch secretions reach a pH of 1.0 (EDMUNDS, 1968) whereas others are neutral, yet toxic enough to repel predatory sunstars and even cause death to neighboring sea anemones, amphipods, and ascoglossans (JENSEN, 1984; AJESKA & NYBAKKEN, 1976).

Other defensive features of opisthobranchs include rapid swimming (HURST, 1968; BICKELL-PAGE, 1989); "fast creeping by producing large direct monotaxic pedal waves" following disturbance (AGERSBORG, 1923); and discharge of stored nematocysts that had been sequestered from cnidarian prey (GRAHAM, 1938; DAY & HARRIS, 1978).

This panoply of defensive mechanisms found in some opisthobranchs supports the idea that they respond to predators with the release of mucus and toxins, and in some cases nematocysts. Presumably the predator is sufficiently discouraged to abandon its pursuit. This deterrent may explain why few predators of opisthobranchs are known. However, in the laboratory the pycnogonid *Anoplodactylus carvalhoi* appears not to be bothered by putative defense mechanisms of the opisthobranch *Dondice occidentalis*. Indeed, it may even take advantage of ceratal autotomy in order to harvest and then consume autotomized cerata.

In June of 1990, numerous specimens of the sea spider *Anoplodactylus carvalhoi* and one nudibranch, *Dondice occidentalis*, were collected from *Eudendrium* sp. under the wharf of the downtown Ft. Pierce marina, St. Lucie Co., Florida. The sea spiders were contained in an aquarium along with cuttings of *Eudendrium*. They were not seen grazing on the hydroid, but because hydroid polyps are known to be the food of congeneric species (RUPPERT & FOX, 1988), it is possible that these polyps constitute a part of the diet of *A. carvalhoi*. The collected sea spiders were robust and thrived under laboratory conditions.

On five occasions I observed sea spiders feeding on polychaetes. When a small yellow sabellid polychaete attached to a hydroid branch was coaxed from its retreat and placed before a sea spider, it was readily snatched by the pycnogonid's chelicerae. The predator inserted its proboscis into a hole that it made at one end of the worm and sucked out the worm's contents.

The attack of *Anoplodactylus carvalhoi* on *Dondice occidentalis* was observed under a dissecting microscope in a dish (11 cm diameter, 5 cm deep) that contained several short snippets of *Eudendrium*. At first the nudibranch wandered about slowly on the bottom of the dish while the sea spider remained motionless. When they were within 4 cm of each other, the sea spider turned and pursued the nudibranch. The sea spider hooked the margin of the nu-

dibranch's foot with the claw of its first leg and drew itself close to the mollusk. At this point the pycnogonid's proboscis faced the nudibranch's venter, and it proceeded to turn the prey over so that its chelicerae came into contact with the dorsal cerata. Each chelicera grabbed a ceras, causing it to autotomize. The sea spider released the nudibranch, which moved off leaving a trail of mucus. Then the predator consumed each ceras, one after the other, by inserting its proboscis into the severed end and sucking out the contents.

This scenario was repeated four times that day by subjecting the same nudibranch to four different pycnogonid specimens. The same set of events took place at each trial, with the exception that in these cases the nudibranch was upright, and thus was not flipped over. Because the sea spiders attacked the nudibranch by surprise, there was no way to determine whether the mucus secretions had any effect on them.

To discover whether the mucus trail could deter pycnogonid pursuit, the following day the specimen of *Dondice occidentalis* was placed in the same dish, but this time with six pycnogonids. The nudibranch was hounded by the sea spiders, and each taxed the nudibranch of two cerata. Although the branches of the *Eudendrium* clipping quickly became gummed up with mucus, the pycnogonids continued making assaults unimpaired. After supplying all six sea spiders with cerata, the nudibranch became noticeably denuded. It eventually died of unknown cause on the third day.

I have been unable to find any reports of adult pycnogonid predation on nudibranchs, but I have noticed an illustration depicting this event in *Invertebrate Zoology* (BARNES, 1987:747).

Acknowledgments

Many thanks to Dr. Richard Fox for identifying the mollusk and to Dr. Kenneth Boss and two anonymous reviewers for commenting on this manuscript.

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BOOKS, PERIODICALS & PAMPHLETS

Atlas of Mediterranean Nudibranchs

edited by R. CATTANEO-VIETTI, R. CHEMELLO & R. GIANNUZZI-SAVELLI. 1990. La Conchiglia, Rome. 264 pp. Price: \$60.00.

One aim common to the dozen or so books on nudibranchs published during the last decade has been the popularization of these mollusks. This atlas certainly achieves that objective for the Mediterranean Sea. The scuba revolution has brought the undersea world within the comprehension of every person so that it is indeed timely to promote its most beautiful, bizarre denizens. This new awareness is exemplified by Philippe Bouchet in his foreword to the atlas wherein he reminds readers that *Peltodoris atromaculata* (as *Discodoris* elsewhere in the book), the nudibranch many divers, myself included, would today judge as the "most common" or "most typical" Mediterranean species, was known only from the unique holotype a little over 30 years ago.

The world may have opened its eyes to nudibranchs, but sadly most of the popular books describing them are slim, soft-covered affairs because publications containing color are prohibitively expensive. Therefore the appearance of this large, hard-covered book is a pleasant surprise. Its publication was apparently funded by the Regional Provincial Authority of Palermo, Sicily.

Physically this book is like Schmekel and Portmann's *Opisthobranchia des Mittelmeeres*, but its approach is more "user friendly."

The format is logical: introduction, checklist of Mediterranean nudibranchs, descriptive text (containing succinct diagnoses of higher taxa), color plates, glossary, and references. The text, which is in both Italian and English throughout, is terse yet sufficient. Subheadings for each species indicate principal synonymy, references to literature, description, radular details, habitat, and known range. The information supplied under habitat represents an invaluable data set for future workers.

The 14 composite color plates illustrate 90 of the 252 species included in the checklist. According to the authors' note at the beginning of the book, these are the most common Mediterranean nudibranchs "or, at least, those whose images could be obtained." The quality of these illustrations is generally excellent, particularly those taken by Giorgio Barletta to whom, along with Mauro Sordi and Tom Thompson, this book is dedicated. Usually there is one color illustration per species, but more are provided for the most variable taxa like *Chromodoris luteorosea*, *C. britoi*, and *Hypselodoris messinensis*.

In contrast to the many excellent or useful aspects of this work, the system of higher classification is likely to mystify general and specialist readers alike. The four tra-

ditional suborders of the Nudibranchia are maintained, albeit with *-ina* suffixes. However, the divisions at the level of superfamily are curious to say the least. For the Arminina, the subdivision Euarminoidea Odhner *in Franc* is rejected both because Arminoidea Alder & Hancock is older and because Euarminoidea is not based on a valid generic name; yet the subdivision Metarminoidea Odhner *in Franc* is retained over its senior synonym Herodoidea (sic) Bergh because the latter is "based on an atypical genus." Both these same two grounds are advanced within the Doridina where Anadoridina Odhner, Eudoridoidea Odhner, and Porodoridoidea Odhner *in Franc* give way to Onchidoridoidea Alder & Hancock, Polyceroidea Alder & Hancock, Doridoidea Rafinesque, and Phyllidoidea Rafinesque although the composition of the first two superfamilies is not Odhner's. (Phyllidoidea, incidentally, is based on an "atypical" porostome *Phyllidia*.) The Aeolidiina is partitioned between the three informal categories "pleuroprocta," "acleioprocta," and "cleioprocta." This higher classification is not the same as that employed in Sabelli, Giannuzzi-Savelli & Bedulli's recently published *Annotated Check-list of Mediterranean Marine Mollusks* though one might expect it to have been for the sake of general readers anxious to place taxa in pigeonholes.

The tangle of the higher classification symbolizes what remains to be uncovered in this fascinating group. However, for the Mediterranean we have at last with this atlas a comprehensive list, a set of fine illustrations, and anatomical data that overcome most of the uncertainties of nudibranch specific identification so prevelant for the earth's other seas.

R. C. Willan

Monograph of Living Chitons

(Mollusca: Polyplacophora)

Volume 4, Suborder Ischnochitonina.

Ischnochitonidae: Ischnochitoninae (continued)

Additions to Vols. 1, 2 and 3

by PIET KAAS & RICHARD A. VAN BELLE. 1990. E. J. Brill, Leiden. 298 pp., 117 figs., 48 maps. Bound, 95 guilders (about U.S. \$54).

This fourth volume of a projected 10-volume set retains the same format as the first three volumes of this extensive review of the Recent Polyplacophora. Each species, placed in geographic order within subgenera, is fully described and well illustrated, but comparative remarks are typically lacking.

About the first one-fifth of the text is devoted to addi-

tional information on taxa covered previously in the series. The amount of this added material is an indication of the advances in polyplacophoran taxonomy over the last few years. The authors must be commended not only for pressing forward with their revision, but also for providing the reader with timely updating of prior volumes. This first section includes the description of eight new species of *Leptochiton*, *Callochiton*, *Chaetopleura*, and *Lepidozona*. Malacologists on the west coast of North America will be especially interested in the introduction (pp. 46–51) of *Lepidozona tenuicostata* and *L. sirenkoi* from Punta Peñasco, Mexico. In contrast to the conclusion of FERREIRA (1983. The Veliger 25:312), Kaas & Van Belle recognize (pp. 33–39) as distinct taxa *Stenoplax rugulata* (Sowerby, 1832) and *S. mariposa* (Dall, 1919) of the eastern Pacific and *S. petaloides* (Gould, 1846) from Hawaii. Based on the work of GOWLETT-HOLMES (1987. Transactions of the Royal Society of Southern Australia 111:105), Kaas & Van Belle (p. 22) accept the placement of *Chorioplax grayi* (H. Adams & Angas, 1864) in the order Chorioplacina Starobogatov & Sirenko, 1975. Study of the type material of *Ischnochiton moreirai* Righi, 1973, has allowed Kaas & Van Belle (p. 52) to assign this Brazilian species to *Connexochiton* Kaas, 1979, previously known by only two species, including *C. bromleyi* (Ferreira, 1985) from Barbados. *Bathychiton biondii* Dell'Angelo & Palazzi, 1988, from the Mediterranean Sea is reported (p. 54) to be a junior synonym of the eastern Atlantic *Connexochiton platynomenus* Kaas, 1979, and *Bathychiton* therefore must be considered a junior subjective synonym of *Connexochiton*. Kaas & Van Belle present intriguing scanning electron micrographs of the radula of *C. platynomenus*, which show an unusual sickle-shaped cusp on each major lateral tooth.

The remaining pages cover subgenera of the genus *Ischnochiton* that are distinguished primarily on the basis of girdle scale shape and size. As a result, *Ischnochiton* s.l. and even *Ischnochiton* s.s. include chitons with tegmental sculpture ranging from quite smooth to heavily ribbed and chitons with greatly differing radulae. The "*Ischnochiton*" problem has perplexed malacologists over the last century, and it appears that a natural classification will become evident only after the utilization of a variety of taxonomic characters, including those from the fields of comparative anatomy and molecular genetics.

Most of the eastern Pacific and Caribbean "*Ischnochiton*" species are included in this volume. These species are placed primarily in *Ischnochiton* s.s., and the use of *Rad-siella* Pilsbry, 1892, promoted by Thorpe (in KEEN, 1971. *Sea Shells of Tropical West America*. 2nd ed.) is not followed. Kaas & Van Belle describe five new species of *Ischnochiton* from different oceans, including *I. chaceorum* from Punta Peñasco, Mexico (p. 167). The Caribbean species of *Ischnochiton* are reviewed without any nomenclatural changes or substantial comment. The authors follow (pp. 93–100) Kaas' earlier conclusion (KAAS, 1972. *Studies Fauna Curaçao* 41:77–89) that *I. striolatus* (Gray, 1828), *I. erythrono-*

tus (C. B. Adams, 1845), and *I. papillosus* (C. B. Adams, 1845) are specifically distinct. After covering other species, they note (p. 113) that *I. niveus* Ferreira, 1987, is "very closely related" to *I. papillosus*, but owing to differences in tegmental sculpture and the major lateral tooth they decline to relegate Ferreira's name to the synonymy of *I. papillosus*.

The systematic text ends with the introduction (p. 254) of the monotypic genus *Leloupia* for *Leptochiton belgicæ* Pelseneer, 1903, known only by the holotype from Antarctica. The generic name honors the late Dr. Eugène Leloup, one of the prominent chiton taxonomists of the 20th century, and to whom the present volume is dedicated.

I have indicated previously (Veliger 29:135, 32:331) in reviews of the first volumes of this well-illustrated series that this work should be part of every malacological library. I have found that I refer to one or more volumes of this series almost on a daily basis, and I eagerly await the completion of more volumes. Even if one had access to a large malacological library, where else could such a wealth of current taxonomic information on the Polyplacophora be obtained? Any malacologist or amateur conchologist with an interest in chitons should seriously consider acquiring these volumes while they are still available.

Robert C. Bullock

Christmas Shells

by FRED E. WELLS, CLAYTON W. BRYCE, JOHN E. CLARK & GLAD M. HANSEN. 1990. Christmas Island Natural History Association, % Australian National Parks and Wildlife Service, Christmas Island, Western Australia 6798, Australia. 99 pp.; color plates. Hardbound. Price: Australian \$13.50 (about US \$10.00).

This attractive, small volume illustrates the majority of marine molluscan species and probably all of the large, common mollusks at Christmas Island, an isolated territory of Australia, some 1400 km from the nearest point on the Australian coast and about 360 km from the island of Java. The book tries to do many things for many people, and for the most part it succeeds, although not without some conflicting pulls and tugs.

The numerous, beautiful color plates, the kind of binding and paper, and the general layout would qualify this book for "coffee table" status, where it would find a pleasant place. But the volume is also intended to be an identification guide. Indeed the illustrations are of sufficient quality to serve for preliminary identification in many instances, but taking the book into the field, as the authors suggest, would likely end its service on the coffee table.

Another conflict with which the authors must try to deal is the conflict between shell collecting, the enjoyment and value of which is promoted by the book, and conservation. Introductory sections of the book stress the need to follow

thoughtful rules of collecting (e.g., turn rocks back over, leave breeding animals alone, limit collecting to one or two specimens per species). These are considered especially important because of the small size of the island and the limited patches of certain habitats—the potential for depleting some habitats of mollusks is great. The concern for conservation is heightened by the intention to change the economy of the island from one dependent on phosphate mining (the mine closed in 1987) to one targeting tourism. This book is intended to increase the enjoyment of visitors to the island's shores, but will also serve as a baseline of sorts for the "pre-tourist" condition. One can only hope that molluscan species listed now as "common" at Christmas Island will remain so in the future. Perhaps the cynics will be more heartened by the note that no marine molluscan species are thought to be endemic to Christmas Island.

The body of the book consists of information on the 379 species of marine mollusks from Christmas Island, including 332 species of gastropods, 42 bivalves, 3 polyplacophorans, and 2 cephalopods. Species are organized by class and family, and for each species a standard set of information is provided: scientific name including author and year, an average size of specimens, an indication of the abundance at Christmas Island (rare, uncommon, common), the usual habitat in which the animal may be found (e.g., in subtidal sand), and a color photograph. Suggestions for further reading in the scientific literature are included with general comments on many families. By and large the color plates are excellent in their detail, color, and sharpness. No specific information on the geographic range of the mollusks found at Christmas Island is provided, except that species occurring also at the Cocos (Keeling) Islands are so noted; all of the molluscan species are said to be widespread in the Indo-West Pacific.

The forematter of the book consists of sections introducing the reader to Christmas Island, the need for conservation when collecting, and how to build and care for a shell collection. The back matter, which includes a glossary and an index to the scientific names of presented taxa, again illustrates the authors' attempts to serve readers of different interests and backgrounds. The glossary includes definitions of such terms as "carnivorous," "class," and "subtidal," while the index includes no vernacular or common names at all, such that a reader faced with a specimen known as a cockle, bubble shell, whelk, or cowry would find no help in the index, even though these terms are used in the text. On the other hand the authors are to be congratulated for not succumbing to the temptation to add contrived vernacular names to the scientific ones.

Purchase of *Christmas Shells* should be seriously considered by anyone interested in mollusks of the Indo-West Pacific, and most certainly by would-be collectors to that area. Those with extra space on the coffee table might also give it a look for the beauty alone.

D. W. Phillips

Northern Abalone, *Haliotis kamtschatkana* in British Columbia: Fisheries and Synopsis of Life History Information

by N. A. SLOAN & PAUL A. BREEN. 1988. Canadian Special Publication of Fisheries and Aquatic Sciences 103: 46 pp. Available from Canadian Government Publishing Centre, Ottawa, Canada K1A 0S9. Price: Canadian \$14.35 plus about \$4.50 shipping and mailing.

The title of this pamphlet accurately describes its content. Sloan and Breen, both veteran researchers of invertebrate fisheries, have compiled an extensive review of the life history and fisheries of *Haliotis kamtschatkana*, also known in British Columbia as the northern abalone and in California as the pinto abalone.

British Columbia populations of *Haliotis kamtschatkana* are emphasized, but information is also drawn from southern populations and from other abalone species. Use of this expanded data set is justified by the authors' conclusion that "much of what is known about other *Haliotis* species is relevant to northern abalone and no striking or unique aspect of the biology of northern abalone has been discovered (p. 40)." Included in the review are information on taxonomy, distribution, aspects of life history (reproduction, pre-adult history, food and growth, competition, predation, and population structure), and fisheries.

With the exception of some recent survey data, no new research results are presented. The authors do, however, identify several fruitful areas for future research, the most important being processes of recruitment, causes of mortality of early life stages, small-scale distribution patterns, and short-term movement patterns.

In short, this synopsis presents much useful and valuable information on abalone. It should be in all institutional libraries and read with interest. For individuals, however, the price may seem rather high for a publication with no halftone plates (except the cover), and the choice of whether the information is worth the cost, approaching \$0.35 per page, will likely be a personal one.

D. W. Phillips

Squid as Experimental Animals

edited by DANIEL L. GILBERT, WILLIAM J. ADELMAN, Jr. & JOHN M. ARNOLD. 1990. Plenum Publishing Corporation. 516 pp. Price: \$75.00 (\$90.00 outside of USA).

As a graduate student at Hopkins Marine Station in Pacific Grove, I remember watching in fascination as hatchlings of the squid *Loligo opalescens* cavorted around dishes of seawater in the teaching laboratory. I remember too that adults of this species, gleaned from sympathetic commercial fishermen, served as the primary protein source for more than one graduate student on a tight budget, and that I nearly started down the research path of squid neurophysiology. Thus, it was with interest and fond memories that I started to read *Squid as Experimental Animals*.

Although the volume contains much information that would be of use to graduate students and researchers on squid physiology, the book was something of a disappointment, among other reasons for its treatment, by many authors, of squid as model experimental systems rather than as interesting animals. Except in a few of the chapters, little of the fascinating flavor of these magnificent mollusks comes through.

The book contains 22 chapters written by 34 authors, and undoubtedly presented an editorial challenge. Even with three editors, however, the volume as a whole still suffers from unevenness, inconsistency, and unfortunate errors. For example, one chapter dispenses with "Evolution and Intelligence of the Cephalopods" in five pages of text plus another page of references, while another goes on for almost 70 pages on "The Cytoskeleton of the Squid Giant Axon." Admittedly, my editorial hackles were raised on the first page of text by the usage of the word "data" as a singular noun, followed by subsequent pages by some inconsistent, and unorthodox, use of capitalization.

Perhaps some of these can be dismissed as stylistic quibbles, but the explanation of the "modern" spelling of the primary squid species that serves as the subject for much of the book, delivered in an authoritative manner with reference to the "rules of zoological nomenclature," warrants a further note so that readers do not believe the incorrect explanation. According to one author "a single *i* is preferred as the suffix in the formation of a scientific name under the *Rules of Zoological Nomenclature*; hence the name *Loligo pealei* for this species . . . (p. 15)." The problem is, of course, that the *Code*, presumably what is meant by the "Rules," makes the above recommendation for the formation of *new* names only. This species, however, was originally named *Loligo pealeii* by Lesueur. Thus, Article 33d unequivocally states "the use of the termination *-i* in a subsequent spelling of a species-group name . . . based upon a personal name in which the correct original spelling terminates with *-ii*, or vice versa, constitutes an incorrect subsequent spelling, even if the change in spelling is deliberate."

The 22 chapters of the 516-page book are apportioned among six parts. Part 1 (60 pages), containing four chapters grouped loosely under the heading of "Evolution, History, and Maintenance," will probably be of most interest to readers of *The Veliger*. Of these, the chapter by R. T. Hanlon describing the maintenance, rearing, and culture of squids is especially good; in addition to delivering on the promise of the title, this chapter also contains several interesting tidbits of information on behavior and natural history. Part 2 (26 pages) consists of only two chapters, one on mating behavior, the other on the embryonic development of squid; these also will likely be of interest. Part 3 (100 pages), with five chapters on neural membranes, and Part 4 (174 pages), with five chapters on cell biology, are geared mostly for researchers in cell biology. These chapters contain a large amount of highly technical information and demonstrate well how useful squids have

become to cell biologists during the past few decades. My primary complaints about these chapters are the general lack of a concise synthesis of the information and the generally insufficient attempts to relate the information to the biology of the animal. Part 5 (69 pages), with the heading of "Sensory Systems," contains three chapters and covers the visual system and statocysts of squids, mostly in relation to their structure and function. Part 6 (61 pages) contains three chapters under the heading of "Integrated Systems." Notable among these are chapters on gas transport in the blood (C. P. Mangum) and locomotory, respiratory, and circulatory integration in these most active of mollusks (R. O'Dor et al.).

Squid as Experimental Animals serves as a state-of-the-art compendium of the enormous amount of information that has been generated during the past several decades on the fine anatomy, cell biology, and physiology of squids. For this the authors and editors are to be commended. Their book should find a useful place on the shelf at the libraries of many research-oriented institutions. Individuals with interests in culturing squids and with research interests in cell biology and physiology are most likely to benefit.

D. W. Phillips

The Marine Flora and Fauna of Albany, Western Australia

edited by F. E. WELLS, D. I. WALKER, H. KIRKMAN & R. LETHBRIDGE. 1990. Volume 1: 1-437. Volume 2: 439-722. Western Australian Museum. Price: about Australian \$75.00.

In January 1988, 31 scientists from Australia and five other countries gathered at Albany, Western Australia, for the "Third International Marine Biological Workshop." The scientists worked at Albany for 18 days and then took specimens and data to their home laboratories, where data and reports were worked on for the remainder of the year. At that time, papers were submitted and reviewed before being accepted for publication.

The two volumes, 721 pages in total, contain 29 research papers from 27 contributors. Of the 29 papers, 13 deal with mollusks, either as the primary subject (10 papers) or in substantial part (3 papers). Eleven of the molluscan papers are contained in Volume 2.

In general the papers are of high quality, attesting no doubt to the skills of the investigators, the workshop organizers, the editors, and the workshop concept of focusing the attention of international experts on a particular subject or area. Many topics are covered, including works on ecology, behavior, physiology, functional morphology, development, and systematics. Four new taxa of mollusks are described: a new family, the cerithioidean family *Plesiostrochidae* by Houbbrick, and three new species of *Sacoglossa* (= *Ascoglossa*), *Volvatella ventricosa*, *Elysia filicauda*, and *Pattyclaya brycei*, all by Jensen and Wells.

These papers contribute greatly to our knowledge of the molluscan fauna of Western Australia (and beyond) and the volumes are highly recommended. If I might lodge one complaint, it would be that not all of the authors seem to have deposited voucher specimens or representative samples at the Western Australian Museum or at some other recognized repository. As expected, voucher specimens were deposited for taxonomic works, and for a few of the others, but representative collections from *all* of the studies should be accessible to scientists now and in 100 years.

D. W. Phillips

**Résultats des Campagnes MUSORSTOM
Volume 7**

coordinated by A. CROSNIER & P. BOUCHET. 1991. *Mémoire du Muséum National d'Histoire Naturelle*, Ser. A, Tome 150. Available from: Universal Book Service, Dr. W. Backhuys, Warmonderweg 80, 2341 KZ Oegstgeest, The Netherlands. Price: 350 Francs plus 10% postage.

Too good to remain hidden by its rather uninformative title, this volume, based on results of deep-sea cruises sponsored jointly by the Muséum National d'Histoire Naturelle and ORSTOM, contains much information of considerable interest to malacologists. Contained are 10 contributed papers on the systematics of deep-sea mollusks of the New Caledonian region. Indeed, all of the papers in the volume are on mollusks, and all but two are written in English. One paper describes chitons, one bivalves, and eight gastropods.

In all, an impressive array of new taxa are described from off New Caledonia, including one new family and subfamily, five new genera, and 90 new species. Kaas describes eight new species and one new genus (*Vermichiton*) of chitons, and Bergmans identifies six species of Nuculidae (Bivalvia), including three new to science. Perhaps the most remarkable systematic find, however, is de-

scribed by Marshall: 55 species of the Seguenziidae (Gastropoda, Archaeogastropoda) are newly recorded from off New Caledonia and the Loyalty Islands. Included in this rich fauna are 50 seguenziid species new to science and two new genera. Warén and Bouchet provide a wealth of anatomical detail to support their formation of a new family, the Haloceratidae (type: *Haloceras*), considered related to the Tonnoidea; of 17 named species in the family, 10 are new. Four new species of Rissoininae are described by Sleurs, and Dolin describes (in French) a new species of *Cypraeopsis* (Ovulidae), a genus previously represented only by fossils. Cernohorsky reports 33 species of Nassariidae from New Caledonian waters; 30% of the recorded species represent extensions of known range and one species is new to science. Lozouet describes (in French) four new species of *Eumitra* (Mitridae), which are the first Recent species of this genus, and Houart describes five new species of Typhinae, all from the deep sea. Harasewych describes three new species and one new genus of columbariform gastropods.

This volume meets the high standards we have come to expect from Philippe Bouchet and the MNHN group. The papers are well written, concise, informative, and well supported. Almost without exception (I will not name the exception) the halftone illustrations, including scanning electron micrographs of radulae, protoconchs, and shells of adults, are superb, sharp and beautifully printed on glossy, acid-free paper.

The impressive array of new taxa described in Volume 7 of *Résultats des Campagnes MUSORSTOM* is a large and significant contribution to what we know about deep-sea mollusks, and suggests, too, how much remains to be learned. Papers in Volume 7 are likely to be cited often, so I am pleased to have a copy on the shelf. I will also look forward to the future volumes that are said to be in press or in preparation.

D. W. Phillips

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e.*, *not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.*, 1953).

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a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra*. *The Veliger* 4:132-134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. *Living marine molluscs*. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135. *In*: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

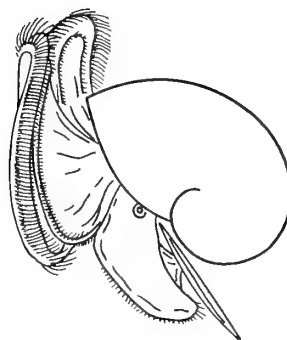
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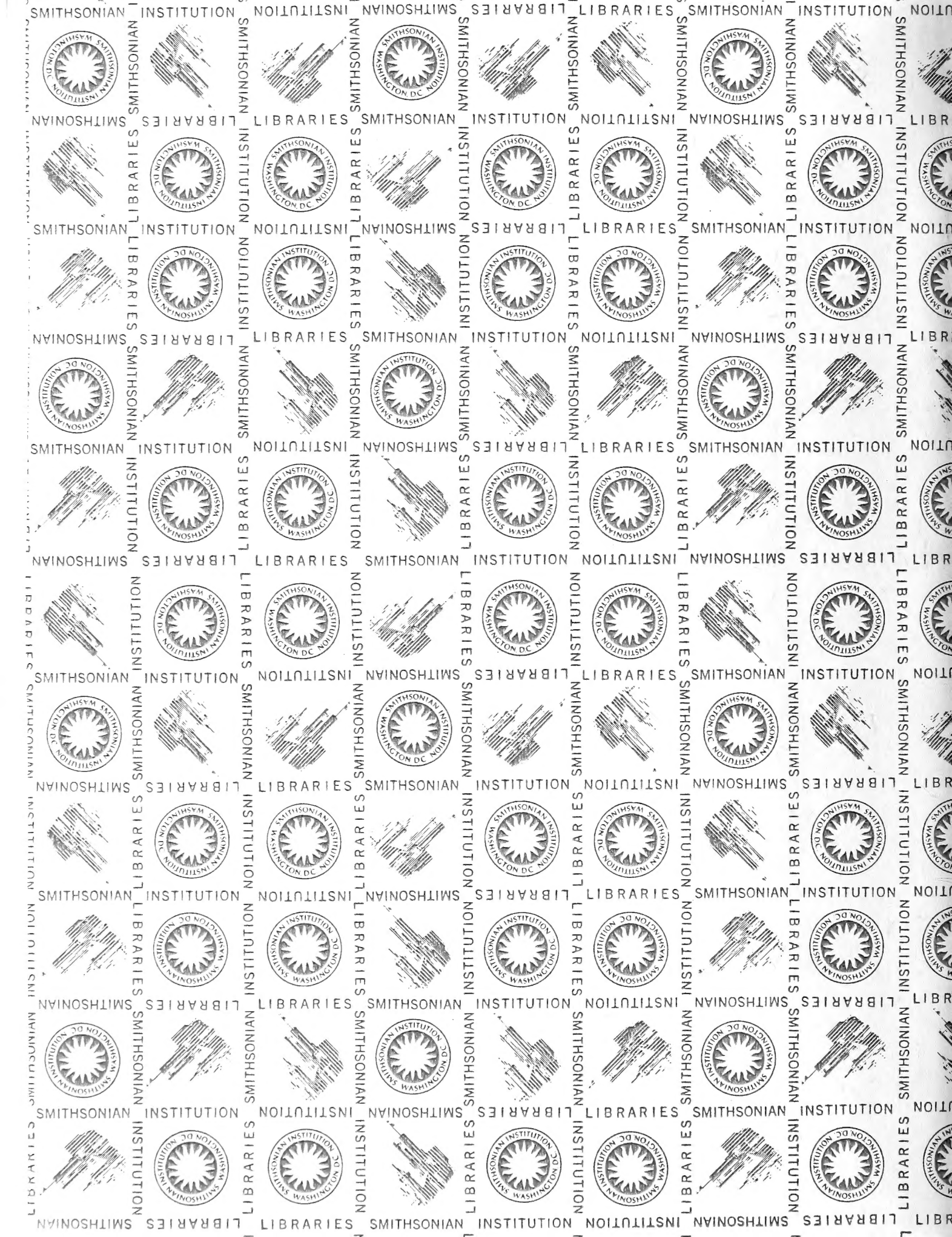
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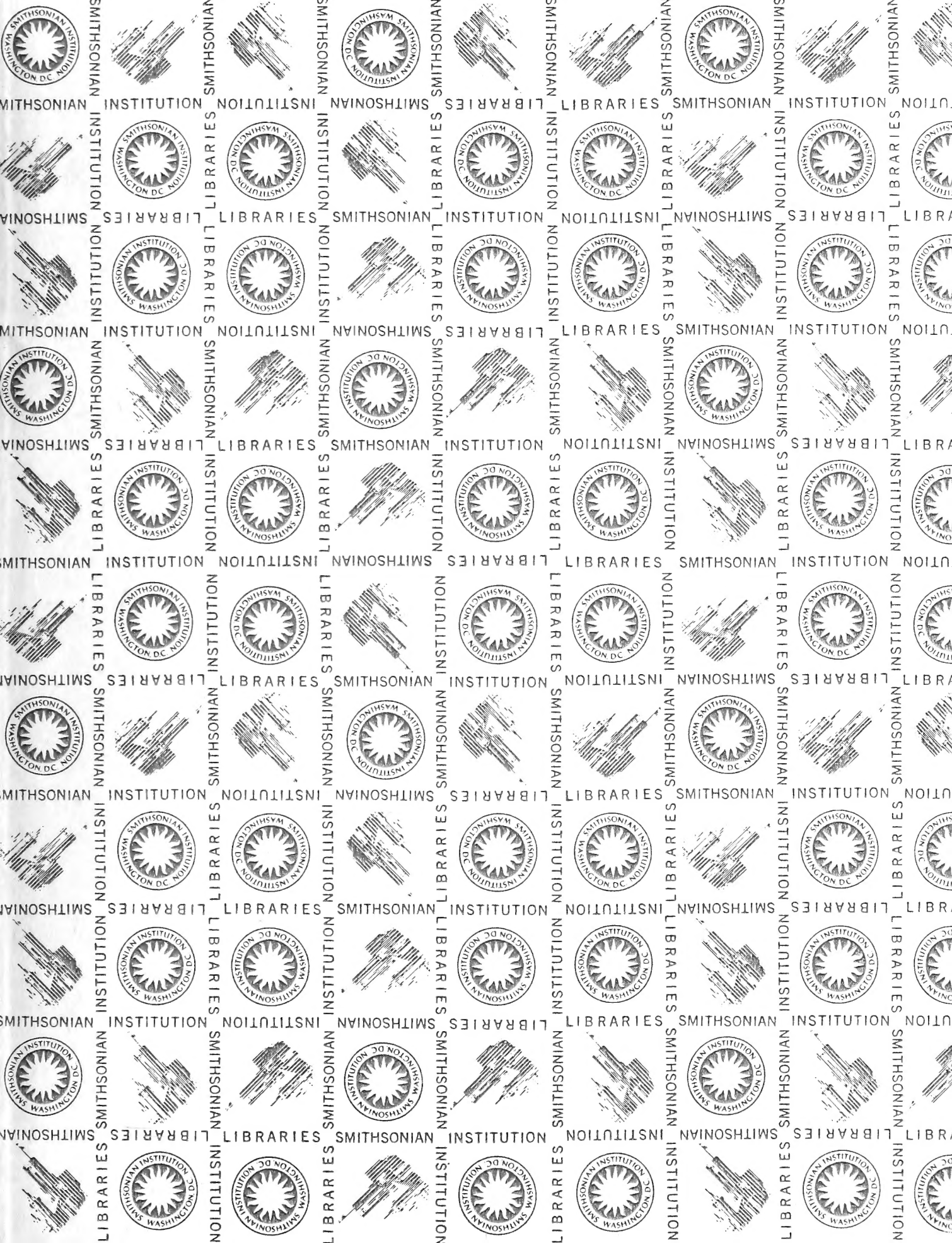
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